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THE SKELETAL ANATOMY OF FLEAS (SIPHONAPTERA)

(WITH 21 PLATES)

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INTRODUCTION

The flea is a remarkable insect. From a much simplified larva having ordinary biting mouth parts, no thoracic legs, and a pair of small peglike struts on the anal segment, it transforms through a pupal stage into an incomparably specialized imago. No part of the external anatomy of an adult flea could possibly be mistaken for that of any other insect. The head, the mouth parts, the thorax, the legs, the abdomen, the external genitalia all present features that are not elsewhere duplicated among the hexapods. As to the relationships of the fleas, the most that can truly be said, notwithstanding the many pages of printed matter that have been devoted to the subject, is that the Siphonaptera are one of the group of insects having papilliform rectal organs, which group includes otherwise the Mecoptera, Trichoptera, Lepidoptera, and Diptera. In common with these insects the fleas have also the type of male genitalia in which the parameral claspers are separated from the aedeagus and appear in the adult as independent appendages of the ninth abdominal segment. The claspers, moreover, are two-segmented, as they are in many of these insects. The mouth parts of the flea, however, combine characters found in Corrodentia, Thysanoptera, and Hemiptera with a great exaggeration of a structure otherwise peculiar to Hymenoptera. The locomotor mechanism, though allowing the flea to walk or run in the manner of other insects, is at the same time specialized for jumping, and many of the thoracic characters are clearly correlated with the leaping function of the legs, particularly the hind legs. Throughout the skeletal anatomy of the flea, however, there are numerous peculiarities that strain the imagination for a plausible explanation, and the complexity of the male intromittent apparatus is almost beyond belief. Internally, on the other hand, the flea is fairly generalized, except for the curious mass of spines in its proventriculus.

For the inception and completion of this study of flea anatomy the writer owes much to Dr. H. E. Ewing of the United States Bureau of Entomology and Plant Quarantine, both for his freely given information on the subject of fleas, and for the use of slide mounts in the Bureau collection. Indispensable for work of the kind on which the paper is based, however, is a supply of liquid-preserved specimens, and for material of this nature the writer is indebted to the Bureau's Division of Insects Affecting Man and Animals, and particularly to Dr. W. L. Jellison of the United States Public Health Laboratory at Hamilton, Mont. Dr. Jellison has generously furnished both slide mounts and alcoholic specimens from his collection, judiciously selected for their value in a comparative study of the Siphonaptera. His slide mount of the sexes in copula, here illustrated (fig. 8), gives perhaps the only information available on the functional action of the male intromittent organ in any flea.

The names of genera and species, and their authors, used in this paper are those given by Ewing and Fox in "The Fleas of North America" (1943). The objective of the work is to interpret the skeletal anatomy of fleas according to general principles of insect morphology; the scope is not sufficient to establish anatomical characteristics of families and subfamilies, a matter left to the taxonomists.

I. THE HEAD

The head of the flea is a highly specialized cranial capsule, and most of its special features are peculiar to the Siphonaptera; but in its fundamental structure the flea head does not differ from the head of any other insect. The head is set closely against the notum of the prothorax (pl. 2 B, N_1), its posterior surface more or less protruding into the latter, and rests below on the anteriorly extended propleura (Pl_1). The rounded or angular dorsal margin of the cranium is continuous posteriorly into the upper contour of the thorax (pl. 1), the neck region being covered by a head flange that overlaps the pronotum. The declivous anterior surface of the head slopes down to the peristomal margin on which the mouth parts are attached. On the sides are deep depressions that ordinarily contain the antennae (pl. 2 A, *Ant*), and just in front of them are the eyes (*O*), when eyes are present. The antennal fossae are defined dorsally and anteriorly by sharp margins, which ventrally run out posteriorly on the upper edges of subantennal lobes (*GeL*) of the genae (*Ge*). Posteriorly also the fossae may have distinct margins, but more generally the fossal walls merge gradually into the cranial walls behind them.

The surface of the flea's head is unmarked by any of the grooves, or sulci (commonly termed "sutures"), that ordinarily demark specifically named regions of the insect cranium; the approximate areas of the frons, clypeus, genae, occiput, therefore, must be determined by general considerations of the head structure, and by muscle attachments. A special feature characteristic of many fleas, however, is the presence of an *interantennal groove* on the top of the head between the upper ends of the antennal fossae (pl. 2 G, *iag*). The groove usually forms on the inner surface of the cranial wall a strong *interantennal ridge* (E, *iar*). In cleared specimens the dark ridge is usually so prominent that it obscures the groove which traverses it, and is more often shown in illustrations than the groove itself (pl. 2, A, B, C, D); in some fleas the groove appears, in fact, to be suppressed. On the other hand, in certain groups of fleas, the groove is widely open, and its anterior lip may be so extended as to overhang the posterior lip (pl. 2 H, *iag*). With such species the head has an appearance of being divided by the groove into an anterior part and a posterior part, and is termed a *caput fractum*. On the contrary, when the groove is narrow or absent the head is said to be a *caput integrum*.

The approximate areas of the frons and the clypeus on the cranium of an adult flea can be determined only by the attachments of the dilator muscles of the cibarium and the pharynx. In insects having a well-defined clypeus and frons, the cibarial dilators always arise on the clypeus, the precerebral dilators of the pharynx on the frons. A vertical section of the flea's head shows that the muscles of the cibarial pump (pl. 6 B, *5*) are attached on the descending anterior part of the head wall. This region is, therefore, the *clypeus* (*Clp*), though students of fleas commonly call it the "frons." Laterally the clypeus is not separated from the genal regions before the eyes (pl. 2 A, *Ge*); anteriorly it goes down to the peristomal margin, where it projects beyond the minute labrum retracted beneath it (pl. 6 B, *Lm*). The precerebral dilators of the pharynx spread over almost the entire upper surface of the cranium posterior to the cibarial muscles (pl. 6 B, *6, 7*), and thus show that this region, usually termed the "vertex," is that of the *frons*. It is to be noted that the interantennal ridge (*iar*) lies between two groups of pharyngeal muscles, and is, therefore, a special feature of the fleas, having no relation to the frontoclypeal ridge or its external sulcus in other insects.

The single eye present on each side of the head in many fleas, lying close before the anterior margin of the antennal fossa, is contained in a deep, strongly sclerotic, cup-shaped inflection of the cuticle (pl. 3 K, *ocu*), penetrated at its inner end by the optic nerve. The cornea (*Cor*) is the true outer covering of the eye, and is circular (pl. 2 A, B, C, L, M, N); the dark area around the cornea, which may be irregular or appear to have a small ventral lobe, is the cuticular eye cup, though its outline is often figured and described as being that of the eye itself. The eye cup is solidly fused with the anterior thickened margin of the antennal fossa (pl. 2 E, pl. 3 E, *ocu*).

The flea's eyes are ventrally displaced ocelli, their ocellar nature being shown both by the retinal structure and by the source of the eye nerves in the brain. According to Hanström (1927) the ocular centers of the flea are in the lower median part of the brain, and lateral optic lobes, from which compound eyes are innervated, are entirely suppressed in the brain of the flea. It is, therefore, not clear how Wagner (1939), basing his statements on Hanström, can make the assertion that the eyes of the flea are transformed compound eyes ("Umbildung der Seitenaugen (Komplexaugen)"). Furthermore, Wagner's own figure of a section of the eye of *Pulex* (1939, fig. 16) shows clearly that the eye has the structure of an ocellus. Hanström, without qualification, calls the flea's eyes "ocelli," and expressly says the compound eyes and their brain centers are gone. Compound eyes if present would not likely be in front of the antennae.

The antennae of the fleas are attached on the cranium laterad of the frons, as in other insects. Wagner (1939) says they are attached on the "vertex," but he misinterprets the frons for the vertex. The antennae are always short, but they are usually longer in the males than in the females. Each appendage consists of a basal *scape* (pl. 3 L, *Scp*), an intermediate *pedicel* (*Pdc*), and a distal *clava* (*Clv*) representing the flagellum of an elongate antenna. The clava consists of nine segments and is supported on the pedicel by a narrow petiole. It varies much in shape in different fleas. Its segmentation is often obscured by a partial union of the segments, but the intersegmental grooves are always distinct on the posterior side and may cut into the clava so deeply as to give the latter a lobed appearance. Large sensory organs of unknown function are sunken into the outer surface of the claval segments. The scape is articulated at its base in the upper angle of the antennal fossa, but it is angulated beyond the articulation in such a manner that, when the antenna is erected, it clears the projecting upper margin of the fossa. In the male flea the antennae may exceed the length of the fossae (pl. 2 F, I). and in dead specimens are more often seen erect than in the female (K, N). The male flea is said (Lundblad, 1927) to use his antennae for holding the female during mating (see page 68).

The antennal fossae are so large that they form deep incisions of the lateral head walls, as is seen particularly when the head is viewed from below (pl. 3 A, B, C, D), or in horizontal section (E, F, G). The convergent inner walls of the fossae constrict the head cavity between them (E) ; in some fleas the walls touch each other, and in some they are united, while in still others, though the walls themselves are separated, they are connected by a transverse bar, the *trabecula centralis* (Wagner, 1927), through the middle of the head (F, H, *tc*). The upper ends of the fossae are connected by the interantennal ridge on the dorsal wall of the head, when this ridge is present (pl. 2 E, *iar*), and the sclerotic cups of the eyes (*ocu*) are fused with the anterior walls.

On the dorsal wall of the head in some fleas, always anterior to the interantennal sulcus when the latter is present, is a small median tooth (pl. 2 I, N, *ct*) known as the "frontal tubercle" ("protectum," or "Stiranzähnchen"). Since the part of the head wall on which the tooth occurs, however, is shown by its muscle relations to be the clypeus (pl. 6 B, *Clp*), the tooth would more correctly be termed a *clypeal tubercle.* The tubercle arises either directly from the head wall, or from within a cuticular depression (pl. 2 J) ; in *Listropsylla dorippe* R., Wagner (1939) says it is protractile from its receptacle. The point is usually turned downward, but may be reversed. The function of the structure is unknown. Wagner points out that the tooth cannot be an instrument for rupturing the pupal cocoon because it is not present in all fleas, and may be present or absent in different species of the same genus.

Characters well known to flea specialists are the rows of strong spines on the anterior part of the head in many fleas, known as *ctenidia.* Most frequently present is a *genal ctenidium* along the lower margin of each gena (pl. 2 B, C, F, G, H, K) ; but the spines may run up before the antennal fossa, forming an *antennal ctenidium.* In a few fleas a *coronal ctenidium* extends vertically on each side from in front of the mouth parts to the top of the head. When the coronal ctenidium is accompanied by an open interantennal groove, the flea's head has the curious appearance of being capped with a spine-fringed helmet.

The posterior and ventral surfaces of the flea's head, which are normally concealed against the prothorax, are the most difficult parts of the cranium to understand, in a morphological sense. Dorsally this region is margined by the head flange, which overlaps the pronotum (pl. 3, A-F, *hf*). The head flange, as noted by Wagner (1939), projects from the anterior (dorsal) margin of the occipital region of the cranium (fig. 1 B, *Oc*). The descending posterior head wall below the flange, normally covered by the prothorax, Wagner says represents the occiput and the postocciput; more precisely, it is the *occiput* (*Oc*) and the *postoccipital ridge* (*PoR*). A true postocciput of the insect cranium is a narrow rim on the occipital margin (fig. 1 A, *Poc*), reflected from the posterior lamella of the postoccipital ridge (*PoR*), that gives attachment to the membranous neck. In the flea (B) a postoccipital sclerotization is absent; the neck membrane arises directly from the base (*b*) of the apodemal postoccipital ridge itself.

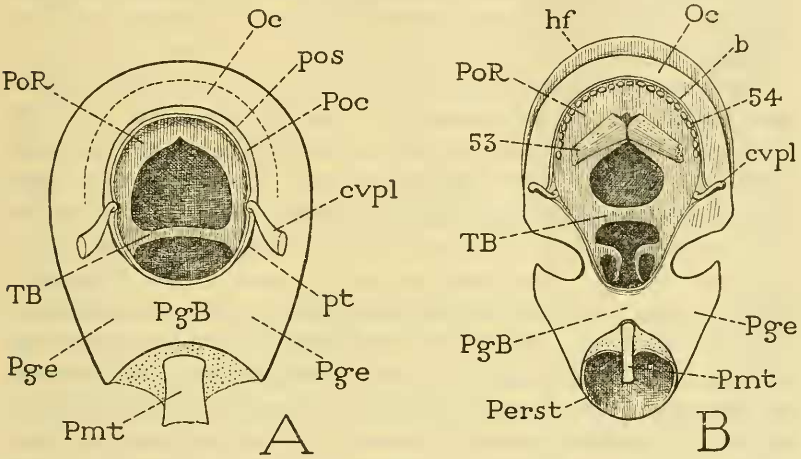

FIG. 1.—Comparison of the posterior structure of a flea's head with that of a more generalized insect.

A, diagram of the posterior head surface of a hypognathous insect having a wide postoccipital ridge (*PoR*), a well-developed postocciput (*Poc*), and a sclerotic bridge (*PgB*) uniting the postgenal areas below the neck foramen. B, corresponding view of the head of *Dactylopsylla bluei* (C. Fox). The flea's head differs from the head at A in the presence of a head flange (*hf*) at the anterior margin of the occipital region, in having a still wider postoccipital ridge (*PoR*), and in the suppression of the postoccipital rim of the cranium, the neck arising directly from the occipital margin (*b*).

b, base of neck membrane; *cvpl*, cervical plate; *hf*, head flange; *Oc*, occiput; *Perst*, peristome; *PgB*, postgenal bridge; *Pge*, postgena; *Pmt*, postmentum; *Poc*, postocciput; *PoR*, postoccipital ridge; *pos*, postoccipital sulcus; *pt*, posterior tentorial pit; *TB*, tentorial bridge; *53*, muscle of cervical plate arising on postoccipital ridge (see pl. 3 J); *54*, bases of thoracic muscles on postoccipital ridge.

When a flea's head is detached from the thorax, the under surface thus exposed appears at first sight to be entirely the posterior and ventral walls of the cranium (pl. 3 D) pierced by the neck foramen (*For*), which is divided into two parts by the transverse tentorial bridge (*TB*). On closer inspection, however, it is seen that the attachment line of the neck (A, B, C, *b*) skirts the foramen anteriorly but diverges far from it posteriorly; the base line of the neck, in other words, separates the head wall into a peripheral, extracervical region, and a central intracervical region. That part within the neck, therefore, is the apodemal postoccipital ridge (*PoR*), which in the flea is unusually large. The extracervical region is a part of the true cranial wall.

The structure of the posteroventral surface of the flea's head is more easily understood by turning the head into a position (fig. 1 B) comparable with that of the head of an ordinary hypognathous insect (A). It is then clear that the dorsal arch of the posterior cranial wall between the head flange (B, *hf*) and the neck (*b*) is the occiput (*Oc*), and that the lateral areas below the level of the neck are the postgenae (*Pge*). The postgenal areas, however, are continuous with each other in a median postgenal bridge (*PgB*) that intervenes between the neck and the peristome (*Perst*), and supports the postmental bar of the labium (*Pmt*). Within the circumference of the neck (*b*) is the broad postoccipital ridge (*PoR*), which, like a diaphragm, cuts down the neck foramen to a relatively small aperture, while the tentorial bridge (*TB*) bisects it into an upper and a lower opening. The occiput and the dorsal part of the postoccipital ridge form a posterior projection of the cranium that descends from beneath the head flange and protrudes into the prothorax (pl. 2 F, G, H, N; pl. 3 H). The ridge usually bears a median crest running upward from the foramen that culminates in a prominent tubercle (*c*), on which are attached a pair of thick muscles (pl. 3 J, *53*) converging from the cervical sclerites (*cvpl*). Above these muscles are the fibers of the longitudinal dorsal muscles from the head to the thorax (*54*), attached anteriorly on the postoccipital ridge in a semicircle just within the dorsal wall of the neck (fig. 1 B, *54*), and posteriorly on the prephragma of the mesothoracic notum.

The tentorium of the flea consists of at least the transverse bridge that crosses the neck foramen (pl. 3 A, B, D, G, *TB*); it probably includes a pair of longitudinal bars, present in some species (F, G, H, *DT*), that are commonly regarded as its anterior arms (see Wagner, 1927). The tentorial bridge of any insect arises laterally, as it does in the fleas, from the postoccipital ridge (fig. 1 A, B, *TB*), since it is formed by the confluence of two opposing tubular ingrowths from the postoccipital sulcus. The points of origin of the component arms usually appear as pits in the sulcus (fig. 1 A, *pt*); in the fleas (B) these posterior tentorial pits are not evident because of the width of the postoccipital ridge and the absence of a postoccipital rim on the cranium. The longitudinal bars referred to the tentorium are shown by Wagner (1939, fig. 8) in *Amphipsylla* to be connected directly with the tentorial bridge; in species examined by the writer they arise from the postoccipital ridge, either near the ends of the bridge, or from the foraminal margins in front of it (pl. 3 G, H, I, *DT*). When these bars are fully developed they extend forward in the head between the antennal fossae and curve laterally to be attached on the genal areas in front of the fossae, and before the eyes, if eyes are present (pl. 3 F, G, H, *DT*). In *Dactylopsylla bluei* the bars arise as thick processes from the foraminal margins (I, *DT*), but they taper rapidly to mere threads that could not be traced to anterior attachments; in *Opisodasys pseudarctomys* vestiges of the bars are present as small projections on the margins of the foramen before the bridge (A).

There is no need to doubt the tentorial nature of the longitudinal bars associated with the tentorial bridge, but the identity of these bars with the usual anterior arms of the tentorium is questionable. True anterior arms should arise anteriorly at or near the upper margin of the clypeus, but these bars in the flea are attached on areas that appear to be the genae, and, moreover, there are no evident pits of invagination at the attachment points. It is therefore to be suspected that the bars in question are *dorsal* tentorial arms and not anterior arms; their lateral positions can be correlated with the ventrolateral displacement of the ocelli. Wagner (1927) says the levator muscles of the antennae take their origins on these bars, and generally in insects it is the dorsal arms of the tentorium, when present, that support the antennal muscles. When these arms are imperfect or absent, however, they could not serve in this capacity, and the writer has observed the antennal muscles of the flea to be attached only on the lower lateral walls of the cranium. While the longitudinal tentorial arms of the fleas are here tentatively regarded as laterally displaced dorsal arms, the anatomical evidence does not fully identify them as such.

The neck of the flea is very short and closely connects the head with the thorax; externally it is entirely concealed by the flange of the head and the prothoracic pleura. On each side, however, the neck membrane contains a small, rod-shaped cervical sclerite, articulated anteriorly on the occipital margin of the cranium (pl. 2 N, pl. 3 A, C, *cvpl*), and posteriorly on the propleuron just below the notum (pl. 2 N, pl. 7 A, D, H). Though the shortness of the neck precludes much movement of the head on the thorax, the strong muscles from the postoccipital ridge to the cervical sclerites (pl. 3 J, *53*) attest that the head has some capacity for independent movement.

II. THE FEEDING APPARATUS

The organs of food ingestion in insects include structures that procure the food from natural sources, and others that convey it into the first section of the alimentary canal, known as the *pharynx*. The procuring organs are the so-called *mouth parts*. The *true mouth* of the insect is the entrance to the pharynx. The feeding organs, therefore, are all extra-oral in a strict sense, though some or all of them may be retracted or concealed within a *preoral cavity* of the head. The intake opening of this cavity then becomes a *prestomum,* which is the functional mouth. Probably all insects imbibe liquid, water if no other, and hence they have a mechanism for sucking. With those insects that feed entirely on liquid food, a part of the preoral cavity, the cibarium, lying between the inner surface of the clypeus and the base of the hypopharynx, is converted into an efficient sucking pump, the *antlia cibarialis.* In some of these insects, furthermore, the pharynx forms an accessory sucking apparatus, the *antlia pharyngealis,* which may itself be differentiated into an anterior pharyngeal pump and a posterior pharyngeal pump.

The mouth parts of an adult flea include a minute *labrum,* a long, slender, unpaired *epipharyngeal stylet,* a pair of maxillae with paired *maxillary stylets,* a small *hypopharynx,* and a simple *labium.* Mandibles are absent in the adult flea, though present in the larva in the form of small, toothed jaws. The sucking apparatus comprises a preoral *cibarial pump* of unusual construction, and a postoral *pharyngeal pump.* The external aperture of the cibarial pump, the prestomum, lies between the labrum and the base of the hypopharynx, but the food is conducted from the feeding puncture into the pump chamber through a channel on the posterior side of the epipharyngeal stylet closed by the appressed maxillary stylets. Since the flea feeds on blood drawn from beneath the skin of the host, it needs puncturing instruments in addition to its pumping and conducting apparatus.

The labrum and the prestomum.—The labrum of the flea (pl. 5 P, Q, U, *Lm,* S) is a very small but usually well-sclerotized triangular lobe hidden beneath the inflected lower margin of the clypeus (pl. 6 A-F, *Lm*). Its apex projects downward, its basal angles are continued into membranous folds that go back to the base of the small hypopharynx (C, E, *Hphy*). The aperture thus enclosed between the labrum above and the hypopharynx below is the prestomum (D, *Prstm*), or entrance to the chamber of the cibarial pump (*CbP*). The aperture, however, is almost occluded by the epipharyngeal stylet (pl. 5 P, *Ephy*), which projects through the prestomum from its own origin on the roof of the cibarial pump (pl. 6 D). No muscles have been observed attached on the labrum in the flea.

The epipharynx and the sucking apparatus.—The median stylet of the flea's mouth parts is a rodlike outgrowth from the clypeal region of the so-called epipharyngeal wall of the preoral food cavity of the head, and may therefore be termed an *epipharynx.* A similarly developed epipharyngeal structure is not known to exist in any other insect, but an epipharyngeal outgrowth from the oral surface of the clypeus is present in most Hymenoptera, and may take the form of a thick pad, or of a large flattened lobe projecting like a long upper lip from beneath the labrum (pl. 6 G, H, *Ephy*) above a similar suboral lobe of the hypopharynx (*hphy*).

The unpaired stylet of the flea was correctly identified as an epipharynx by the British Advisory Committee on Plague Investigations in India (1906), and its epipharyngeal nature has been confirmed by Nitzulescu (1927); in a recent paper by Dampf (1945) it is described as an epipharynx. Jourdain (1899) believed the organ to be a sucking tube prolonged from the lips of the mouth, and named it a "syringostome." Packard (1894) strongly contended that the median stylet is the hypopharynx, but on the erroneous idea that it gives passage to the salivary duct. Fox (1925) terms it an epipharynx, but most other writers on medical entomology or general insect anatomy, and nearly all flea taxonomists have regarded it as the labrum, probably because Heymons (1899) had asserted that the median stylet of the adult flea is formed within the labrum of the pupa. Landois (1866) noted that the basal part of this stylet within the head is "flaschenartig erweitet," and is followed immediately by the pharynx ("Schlund"). Seeing the same thing, and observing the cibarial muscles inserted on the upper wall of the flask-shaped enlargement, the present writer in a recent paper (1944) mistook this basal structure for the cibarial pump itself, and concluded that the emerging stylet must be the hypopharynx, thus adding one more error to the long list of errors already published on the flea's mouth parts. The "flask" turns out to be only half a flask; its lower side is missing.

The epipharyngeal stylet is a somwhat sinuous rod, seen, in a front view of the head (pl. 3 M, O, *Ephy*), issuing from beneath the clypeus and extending downward between the maxillary stylets (*Lc*) to the tips of the latter. The stylet is usually armed on its exposed anterior surface with a row of widely spaced nodules, varying in size and number in different fleas (pl. 5 H, I, J, L, M), being in some large and toothlike (M), in others hardly perceptible (J) or entirely absent (K). The apex of the stylet is always blunt. On the posterior surface a pair of transparent marginal flanges (pl. 5 N, *f*) forms a median gutter (*fc*) running the entire length of the stylet.

At its base the epipharyngeal stylet appears to be formed by the confluence of four trabeculae, a dorsal pair and a ventral pair (pl. 5 R). The upper trabeculae arise from the roof of the preoral cavity shortly behind the base of the labrum (U). The thicker lower trabeculae are continuations from the sides of a large, strong, oval or pear-shaped sclerotization (*g*) forming a loop in the epipharyngeal wall between the labrum and the mouth of the pharynx (*Mth*). The upper side of this epipharyngeal loop is roofed by an elastic membrane (U, *h*), on which is inserted a compact group of muscle fibers (K, *5*) arising on the clypeal area of the cranium (pl. 6 B, C, D, F). The cavity of the loop is open ventrally, and in its posterior wall is the mouth of the pharynx (pl. 5, R, U, *Mth*). To visualize this unique structure on a larger scale, imagine a long-handled frying pan impressed upside down into the roof of the oral cavity of a hippopotamus, with the handle projecting out of the animal's mouth. The functional entrance to the mouth would then be between the pan handle and the tongue, as in the flea it is between the epipharynx and the hypopharynx; but the analogy is not complete, since the gullet of the flea does not open in the usual place at the base of the tongue, but from the inner end of the inverted epipharyngeal "pan."

The cavity within the basal loop of the epipharyngeal stylet is a shallow upper compartment of the chamber of the cibarial pump (pl. 6 D, *CbP*), and the muscles inserted on the dorsal wall are the usual clypeal dilators of the pump (*5*). The floor of the pump chamber is the sublying surface of an extensive basal plate of the hypopharynx (*Hphy*). This plate is connected with the sclerotic epipharyngeal loop above it by a delicate membrane (*C, i*) continuous from the lateral margins of the prestomum. The food entrance to the pump is the passage between the epipharyngeal stylet and the hypopharynx (indicated by an arrow in D), which is a continuation of the food canal between the epipharyngeal stylet and the maxillary stylets. The part of the hypopharyngeal plate that forms the floor of the cibarial pump (E, *Sit*) corresponds with the *sitophore* on the base of the hypopharynx in more generalized insects. The unique feature in the sucking apparatus of the flea is in the position of the true mouth opening (D, *Mth*), or entrance to the pharynx (*Phy*), which is in the epipharyngeal compartment of the pump and not at the base of the hypopharynx. The sectional view of a flea's head given by Weber (1933, fig. 100) errs in showing the food canal of the stylets leading through the cibarial pump directly into the pharynx.

The pharynx of the flea forms a second pump lying between the cibarial pump and the brain (fig. 6 B). In cross section the pharynx is U-shaped, the dorsal wall being deeply inflected; the dilator muscles (*6, 7*) are precerebral, though in their origins they spread over most of the dorsal wall of the cranium. In some fleas, as in *Hystrichopsylla,* the postcerebral part of the stomodaeum forms apparently a second pharyngeal pump, which is star-shaped in cross section (pl. 3 F, *pPhy*) with opposing groups of dilator muscle fibers converging from the head walls.

The maxillae.—The maxillary appendages of the flea include the large, palpus-bearing lateral lobes of the mouth parts generally termed "the maxillae," and the paired stylets commonly regarded as "mandibles." Dissection easily reveals that the two structures on each side are parts of one organ (pl. 4 D, E, L, M, O, P, S, *MxL, Lc*). The articulation of the basal arms of the stylets on the lobes, and the origin of the protractor muscles of the stylets (*41*) within the lobes can leave little doubt that the stylets are the maxillary *laciniae.* The structure is entirely comparable to that of the maxillae in Corrodentia, Thysanoptera, and Hemiptera. Even in cleared whole specimens the articulation of the basal arm of the lacinia on the maxillary lobe can be seen distinctly (pl. 6 A, *lvr*), and yet it has been represented as if articulated independently on the cranium (see Weber, 1933, fig. 100). The idea that the paired stylets of the flea are mandibles seemed to be confirmed by Heymon's (1899) assertion that they are developed within the mandibles of the pupa. Börner (1904), however, observing the basal connections of the stylets with the maxillae, contended that the paired stylets of the adult flea are the lacinial lobes of the maxillae. There can be no question concerning the anatomy of the adult organs; their ontogeny should be reinvestigated.

The large lateral lobes of the maxillae, since they bear the palpi and contain the protractor muscles of the laciniae, are, at least in part, the *stipites;* it is possible that their terminal parts may represent the galeae, but of this there is no evidence. The stipital lobe presents usually a triangular outline in side view with the apex downward (pl. 4 A, C. E, H), but it has a broad anterior surface (pl. 3 M, N, O, *MxL*), which generally ends below in a rounded or truncate margin, though it is sometimes sharply tapering (pl. 4 G). The apical part of the lobe is apparently of the nature of a flange (pl. 4 M, *d*); it is solid, often transparent, and usually thins down to a knifelike edge (O, S), which may be toothed (F). This apical flange is so consistently present on the maxillary lobe that it may be suspected of having some specific function, but observations have revealed no use made of it during feeding. The bases of the maxillary lobes are attached directly on the lateral margins of the peristome, but so far forward that their mesal angles all but meet at the midline in front (pl. 3 M, O). Cardines are absent; they cannot be supposed to be included in the lobes, because the laciniae could be articulated only on the stipites, nor can the lacinial arms be cardines, because a cardo never has muscles arising in the stipes. No muscles from the head have been observed attached on the maxillary lobes. The long four-segmented palpi are seated on the bases of the stipital lobes, their muscles arise within the latter (pl. 4 L, M, P, S, *35*).

The exposed parts of the maxillary laciniae are long thin blades slightly convex on their outer surfaces, concave on the inner surface, and traversed each by a strong midrib (pl. 4 D, E, I, K, L, O, P, S, *Lc*). The distal two-thirds of the outer wall of each stylet, in all species observed, is armed with four rows of denticles having their points turned upward (N, Q, R). The tip of the blade is blunt, sometimes squarely truncate, and bears several small projections (J, N, Q, R). In the natural position, the two blades lie side by side with their concave surfaces opposed and partially enclosing between them the epipharyngeal stylet. The three stylets thus form an epipharyngeo-lacinial tube (fig. 2 E), the lumen of which is the food canal (*fc*) through which the blood is drawn up to the mouth by the sucking apparatus in the head. The stylet fascicle is ordinarily held in the labium.

At their proximal ends the maxillary stylets are bent back abruptly below the head and become thickened to form the basal arms that serve as levers for the movements of the blades (pl. 4 I, K, *lvr*). The recurved upper ends of the blades where they join the levers are twisted in such a manner that their posterior parts are turned mesally and horizontally beneath the hypopharynx. The laciniae thus compose here a channel that contains not only the base of the epipharyngeal stylet, but also the short, decurved hypopharynx. By this arrangement, the food passage between the epipharynx and the lacinial blades is not interrupted at the bases of the latter, but is carried on over the hypopharynx into the lumen of the sucking pump (pl. 6 D).

The position of the hypopharynx between the bases of the lacinial blades suggests that the saliva discharged from the salivary orifice on the decurved tip of the hypopharynx is received into the food canal. Kraepelin (1884) described narrow grooves near the posterior edges of the inner surfaces of the lacinial blades ("mandibles") that serve for the distal conduction of the saliva, but he did not observe the hypopharynx, and he claimed to have followed the salivary grooves into the head and even to the thoracic salivary glands. The presence of salivary canals on the laciniae, however, is reaffirmed by the Advisory Committee on Plague in India (1906). The canals cannot be seen with certainty in whole specimens, and the writer has not made microtome sections, but there is no reason to doubt their existence.

The lever arms of the laciniae, as already noted, are articulated on the bases of the respective stipital lobes. Each lever is movable by opposing levator and depressor muscles, which communicate movements of protraction and retraction to the lacinial blade. The lacinial protractors arise in the maxillary lobe, usually as two sets of fibers (pl. 4 M, O, S, *41a, 41b*), but in some cases only one muscle was observed (L, P, *41*). These muscles evidently correspond with the usual stipital muscles of the lacinia in any generalized insect; they have acquired a reversed position and a protractor function in the fleas by reason of the recession of the lacinial base on the stipes. On the opposite side of the lever are attached three muscles (pl. 4 L, O, S, *32a, 32b, 32c*). These muscles collectively are comparable with the cranial flexor muscle of an ordinary lacinia, though the single fiber bundle usually present is represented in the fleas by three groups of fibers with different origins on the cranial wall. Two of these muscles are attached on the head of the lever (*32a, 32b*), and are therefore "retractors" of the lacinial blade in the sense that their contraction is exerted against the lever; their actual effect, however, when the flea is engaged in making a feeding puncture and the stylets are anchored in the skin of the host, is to pull the head of the flea downward. The third muscle of this group (*32c*) is attached on the base of the lever proximal to the stipital articulation, usually on a strong basal process of the lever, and hence would appear to be a protractor of the stylet; but probably its most important function is that of swinging the stipital lobe backward into the horizontal position beneath the head assumed by the lobe and palpus preliminary to feeding (fig. 2 D).

The hypopharynx and the salivary pump.—Some of the earlier students of flea anatomy, including Heymons (1899), denied the existence of a hypopharynx in the fleas, but later investigators have noted that the organ is distinctly present, though very small. The exposed part of the flea's hypopharynx is a flat, sharply tapering, strongly sclerotized, decurved projection from the lower lip of the prestomum (pl. 6 C, D, E, F, *Hphy*). It lies close beneath the base of the epipharyngeal stylet, and is inserted into the food canal between the recurved bases of the maxillary stylets (fig. 2 C). It contains the exit canal of the salivary pump (pl. 6 D, E, *SlP*). From the base of this small external lobe of the hypopharynx there is continued into the head a large horizontal plate (pl. 5 W; pl. 6 C, D, E, F, *k*). The anterior part of this plate forms the floor of the cibarial pump (pl. 5 W; pl. 6 E, *Sit*), which is the sitophore on the base of the hypopharynx in generalized insects; the posterior part of the plate is expanded beyond the pump into a broad, decurved apodemal lamella with inflected lower margins that enclose a ventral pocket (pl. 5 T, V), within which arise the dilator muscles of the salivary pump (*18*). The anterior angles of the hypopharyngeal plate are in some cases prolonged into a pair of lateral arms giving attachment to small muscles arising ventrally in the head (T, W).

The salivary ejection pump is a thick-walled ampulla firmly affixed in a vertical position to the under surface of the hypopharyngeal plate at the base of the free lobe of the hypopharynx (pl. 6 D, E, F, *SlP*). The ampulla is an enlargement of the salivary canal of the hypopharyngeal lobe turned down at a right angle to the latter, and receives the salivary duct in its lower end (D, E, *SlDct*). The dilator muscles of the pump, arising in the ventral pocket of the hypopharyngeal plate (pl. 5 T, V, *18*), are inserted on an inflection of the posterior wall of the ampulla. Contraction of the muscles effects a retraction of the pistonlike inflection, which latter, on relaxation of the muscles, springs back by its own elasticity and presumably ejects the saliva from the exit canal (*sc*) of the hypopharynx.

The labium.—The labium of the flea is a relatively simple appendage having a pair of long palpi but no ligular lobes (pl. 5 A-F). The free part of the organ includes the prementum (*Prmt*) and the palpi (*Plp*). The postmentum (*Pmt*) is a rodlike sclerite in the peristomal membrane based on the postgenal bridge of the cranium (pl. 6 B, D, *Pmt*). Its distal end supports the prementum, and gives attachment to a muscle arising in the latter (pl. 5 B, E; pl. 6 B, D, *45*). In the flea this muscle acts as a productor of the prementum. The prementum has a wide channel on its anterior surface (pl. 5 A), and its distal end is deeply notched between the bases of the palpi (A, C, *e*). The palpi are flattened from side to side, and usually have three or five segments (pl. 5 A, B, D, E) but in *Echidnophaga* the very short palpi are unsegmented (C, F). The labium serves to ensheath the stylets, which are held in the channel of the prementum and between the closely appressed palpi (pl. 3 O; pl. 5 G).

The mechanism of feeding.—When a starved cat flea is allowed to feed, it becomes oblivious to everything but the prospect of blood. Hence, if a forefinger is offered it as a food source, the flea may be observed leisurely in any position under the microscope, even with a strong spotlight turned on it. Preliminary to making a feeding puncture, the maxillary lobes and their palpi are turned horizontally backward beneath the head, while the stylets and the ensheathing labium are directed straight down (fig. 2 C, D). Then, lifting its head slightly, the flea may make a few thrusts here and there with the stylets, until the latter, apparently, prick the skin and secure a hold by their tips. At once the stylets begin to sink into the puncture with a slow, even movement, unaccompanied by any appearance of effort on the part of the flea; the head descends as if drawn down by the penetrating stylets, until it rests against the feeding surface (B). As the distance between the flea and the host shortens, the labium, which at first fully ensheaths the stylets, is bent *forward* with an angulation between the prementum and the palpi (A), the stylets being now held proximally in the deep notch of the prementum (F, *e*), and distally between the tips of the palpi. Soon, however, the palpi lose their hold on the stylets and spread laterally (G) or turn backward beneath the head (B) as the stylets complete the penetration. The body of the flea is finally tilted upward on the head and remains in this position until the stylets are to be withdrawn. The legs serve merely as props for the body; the claws take no firm hold on the support during the act of puncturing.

No observations have been made on the feeding act of other species of fleas, but the general likeness of the puncturing apparatus leaves little doubt that the procedure is essentially the same in all. In the sticktight flea, *Echidnophaga gallinacea* (Westw.), however, the labial palpi are so short that they cannot fully ensheath the long stylets (pl. 1 D, G). Specimens of this species forcibly detached from the host often have a small disk of skin impaled on the upper parts of the large, strongly armed stylets, and in such cases the stylet fascicle is held in the notch of the labial prementum (pl. 5 C, *e*), but the short, unsegmented palpi project straight forward between the head and the disk of the host's skin.

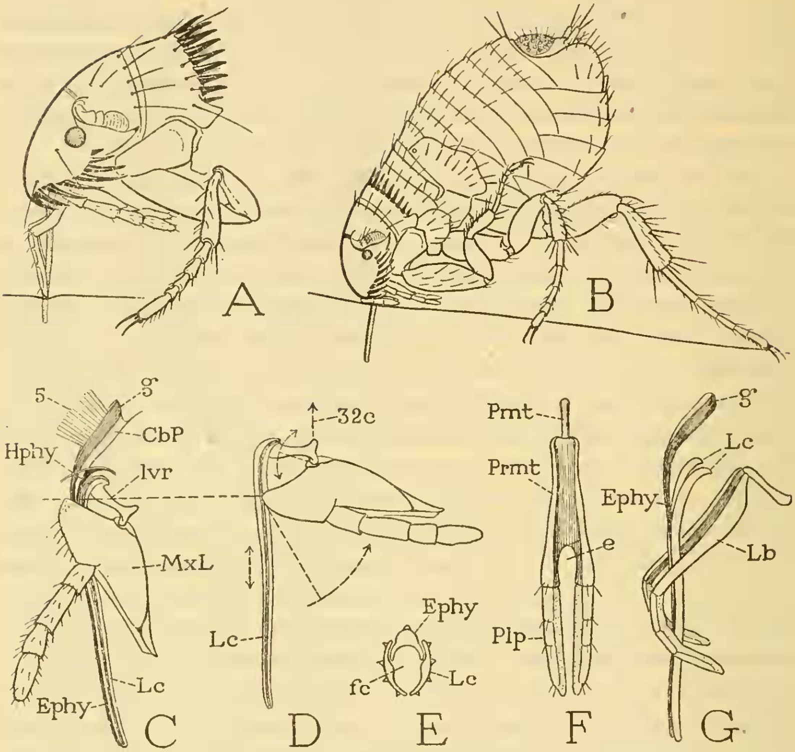

FIG. 2.—The cat flea, *Ctenocephalides felis* (Bouché), in feeding attitudes, and the mechanisms of the feeding apparatus.

A, the head of a flea with the stylets partially inserted, the labium angulated forward. B, a flea with the stylets fully inserted, the labial palpi bent back flat against the feeding surface. (The tilt of the body and the disposition of the labial palpi and the legs are variable in different individuals.) C, the left maxillary lobe and the stylets in an ordinary nonfeeding position, together with the cibarial pump and the hypopharynx. D, the left maxilla in an active puncturing position, the lobe and palpus swung back probably by the basal muscle of the lacinial lever (*32c*); the lever revolving up and down on its basal articulation with the maxillary lobe imparts a back-and-forth movement to the lacinial blade. E, diagrammatic cross section of the stylet fascicle, showing the food canal (*fc*) enclosed by the epipharyngeal stylet and the blades of the maxillary laciniae. F, the labium, anterior view. G, the labium and stylets during insertion of the latter, the stylets held in the notch of the labial prementum as the palpi spread laterally and turn backward.

CbP, cibarial pump; *e,* notch of prementum; *Ephy,* epipharyngeal stylet; *fc,* food canal; *g,* base of epipharyngeal stylet; *Hphy,* hypopharynx; *Lb,* labium; *Lc,* lacinia; *lvr,* lacinial lever; *MxL,* maxillary lobe; *Plp,* palpus; *Pmt,* postmentum, *Prmt,* prementum.

Muscles.—5, dilators of cibarium; *32c,* reductor of maxillary lobe.

The mechanism of the feeding apparatus is fairly simple. The posterior revolution of the maxillary lobe (fig. 2 D) is effected evidently by the muscle (*32c*) inserted on the basal process of the lacinial lever (pl. 4 O, S), since no muscles have been observed attached directly on the lobe itself. The palpus is independently movable by its own muscles. The vertical position assumed by the stylets preparatory to puncturing is perhaps brought about by movements of the labium, though in a dead flea the stylets automatically swing forward when the maxillary lobes are pushed backward. The epipharyngeal stylet is immovably affixed on the head; the maxillary stylets are capable of back-and-forth movements transmitted from the levers. Each lever revolves on its articulation with the maxillary lobe (fig. 2 D), the up-and-down movements being produced by the opposing muscles inserted on it (pl. 4 O, S, *32a, 32b,* and *41a, 41b*). The lacinial movements were not visible in the feeding fleas observed, but it is most probable that they consist of successive short thrusts of the blades alternately on opposite sides, as in the piercing organs of other insects. Each stylet, inserted a little beyond the other, by means of the teeth on its outer surface holds the new position against the pull of the retractor muscles, which, instead of withdrawing the stylet, brings the head down and thus stretches the protractor muscles of the other stylet. If the stylets work in unison a jerky movement of the head should result. The distance that each stylet can enter at one thrust is the contraction length of the operating muscle; it is the rapid repetition of minute strokes that enables the delicate stylets to penetrate the tough skin of the host, a feat that would be impossible by pushing continuously on the bases of the stylets. The action is quite comparable to that of a pneumatic drill used on city streets for boring into hard concrete, or even that of driving a nail by a succession of taps with a hammer.

The passage through which the blood is drawn up to the head is the tubular canal formed by the embrasure of the lateral flanges of the epipharyngeal stylet between the concave inner surfaces of the maxillary stylets (fig. 2 E, *fc*). At the upper end of the stylet fascicle, where the blades of the maxillary stylets turn back to the levers (C), the tapering, decurved hypopharynx (*Hphy*) is inserted into the food canal to complete the floor of the passage into the chamber of the cibarial pump (*CbP*). The fleas watched in the act of piercing were not able to penetrate the finger epidermis to a sufficient depth to draw blood, and hence whatever behavior may accompany the intake of blood was not observed. The extraction of the stylets required a small struggle on the part of the fleas, which latter turned, twisted, and pulled with considerable force before the stylets were released.

III. THE THORAX

The thorax is an important part of the flea's anatomy; though the flea has lost its wings, it has made of its legs an efficient substitute. Hence, in studying the thorax of the fleas, we must recognize the fact that its distinctive features are adaptations for jumping, and that consequently the flea thorax differs in many respects from the thorax of flying insects. Yet, since modern fleas are almost certainly descended from winged ancestors, the thorax still retains the fundamental thoracic structure characteristic of pterygote insects in general.

Concrete evidence of the winged ancestry of the fleas may be seen in the presence of apparent wing vestiges on the mesothorax in the pupa of certain species of modern fleas (pl. 8 F). These "wing buds," which were first noted by Sharif (1935, 1937), are conical outgrowths of the pupal integument suggestive of the wing rudiments of insects in which the wings develop externally, and there is no reason for doubting that they are true wing vestiges. Though Sharif says the "wing buds" of *Nosopsyllus fasciatus* (Bosc) develop on the "pleural region" of the mesothorax, his sectional figure (1937, fig. 82) shows them as folds of the tergal margins above the pleural areas, and therefore having the normal position of wings. Since the wing vestiges occur only on the mesothorax, some will see in this fact evidence of the derivation of fleas from Diptera, but the structure of the flea's head, mouth parts, and male genitalia is not in conformity with such a deduction. Ontogeny does not necessarily repeat the whole ancestral story; the presence of wing vestiges on the pupal mesothorax may represent in the fleas simply the last stage in the elimination of the organs of flight that accompanied the evolution of the legs into organs for jumping. The hind legs and the metathorax are the parts most highly modified for leaping, so probably the metathoracic wings were the first to be lost, and are not known to be recapitulated in ontogeny. The large size of the metathorax in the fleas argues against the derivation of Siphonaptera from Diptera.

The flea's thorax is compact, closely united at one end with the head, at the other with the abdomen; its segments have little individual movement. The metathorax is not always the largest of the three segments, but it is the most highly elaborated, because the hind legs are the principal jumping organs, and their upward thrust is imparted directly to the metathoracic pleura. Even in the less active fleas, such as *Echidnophaga* and *Tunga,* in which the thoracic segments are narrow and closely crowded, the much-reduced metathorax still retains the structure characteristic of this segment in other fleas.

The thoracic segments, though closely united by the conjunctival membranes, are more securely held together by pairs of small connective sclerites resembling the cervical plates that link the prothorax to the head. These thoracic *link plates* lie laterally in the conjunctivae, where each articulates anteriorly with the pleuron of the segment in front, and posteriorly with the notum of the segment behind (pl. 7 J, L, P; pl. 8 B, C, J, M, N, O; pl. 9 C, H, I, K, *1lpl, 2lpl*). The link plates between the prothorax and the mesothorax contain the first pair of spiracles (pl. 14 A, *1Sp*), the second spiracles lie in the membrane below the plates of the second pair (D, *2Sp*). No muscles were observed attached on the first link plates but on each plate of the second pair is inserted a relatively large muscle from the middle coxa (D, *70*).

The prothorax.—Two principal plates are involved in the composition of the prothorax. One is a simple tergal plate, or notum, arched over the back (pl. 7 A, D, H, N_1) ; the other is a composite pleurosternal plate lying horizontally below the notum and supporting anteriorly the fore legs.

The pronotum lies immediately behind the head, its anterior margin is overlapped by the head flange. Beneath the flange, the notal margin is inflected, not in the form of a phragma as in the other two thoracic segments, but as a mere infolding (pl. 7 G, *m*) that produces a recess into which is inserted the occipital arch of the head (pl. 3 H). The rear margin of the pronotum in many fleas bears a ctenidium of strong, spinelike processes (pl. 7 A, D, G, H). Students of fleas are concerned with the question as to whether the ctenidial processes are large setae or true spines. A seta, by definition, is a unicellular outgrowth of the body wall, a spine is a multicellular structure. The nature of the ctenidial processes, therefore, can be determined only by a histological study of their structure in a developmental stage, and no such study apparently has been made on them. The presence of haemocoele canals in the cuticle supporting the ctenidia (pl. 7 I) is no criterion, since all cuticular outgrowths must have, at least in their formative stages, some connection with the body cavity.

The pleurosternal plate of the prothorax presents ventrally a broad, flat or rounded sternal surface (pl. 7 E, S_1), and laterally on each side a triangular pleural surface (D, F, H, *Pl*). There is no line of separation between the component parts, but in some cases a lengthwise ridge of the pleuron possibly separates an episternal area above it (A, *Eps*) from an epimeral area (*Epm*) below it. The pleuron tapers anteriorly to its connection with the fore coxa. The pleurocoxal articulation consists of a pivot on the upper edge of the small basal foramen of the coxa (pl. 7 B, *l*) and a receptive acetabulum on the pleuron (C), an arrangement just the reverse of that which ordinarily hinges the leg to the body. The cervical sclerites articulate with the episternal margins of the propleura near the lower anterior angles of the notum (A, D, H, *cvpl*). On the broad posterior ends of the pleura are attached the spiracle-bearing link plates (A, *1lpl*) between the prothorax and the mesothorax. The sternal surface of the pleurosternal plate is undivided, but the sternum bears on its posterior margin a large apodemal structure (E, F).

The mesothorax.—The middle segment of the flea's thorax has no pronounced angulation between the notum and the pleura, as in the prothorax; on each side, the notum, the pleuron, and the coxa are in vertical alignment, or nearly so, one above the other (pl. 7 J, L, N, P). The notum is an independent plate; the pleura and the sternum are always united, but the union is only an anterior connection on each side (K, M, O), so that there is little confusion as to the pleural and sternal areas.

The mesonotum is a simple, arched plate with a wide posterior flange (pl. 7 J-P, N_2); it has no trace of a sulcus or ridge dividing it into scutal and scutellar areas characteristic of the notum of wing-bearing segments. The lower margins of the plate are closely connected with the pleura, and are slightly overlapped by the latter posteriorly. On its anterior margin the mesonotum bears a large, thin, vertical phragma (pl. 7 K, M, O, *1Ph*) that reduces the body-cavity passage from the prothorax into the mesothorax to the relatively small space between the pleura. The thickened lower edge of the phragma gives the appearance of a transverse bar between the ventral angles of the notum, and probably serves as a brace between the side walls of the segment. At its lateral extremities are articulated the posterior ends of the link plates between the prothorax and the mesothorax (pl. 7 L, P; pl. 8 A, *1lpl*). Ordinarily, in winged insects, the size of a phragma is proportional to the size of the dorsal muscles of the mesothorax or the metathorax. In the fleas these muscles are relatively small because of the absence of wings, but the mesonotal phragma gives attachment to a large, semicylindrical mass of muscle fibers coming from the postoccipital ridge of the head (pl. 3 J, *54*).

The pleuron of the mesothorax is a broad lateral plate between the notum and the coxa, united at its lower anterior angle with the anterior end of the sternum (pl. 7 J-P, *Pl*). The surface of the plate lacks the usual pleural sulcus that ordinarily divides the pleuron into an episternum and an epimeron; posteriorly the plate is produced into a wide flange narrowly continued around the dorsal margin, where it overlaps the lower edge of the notum; the thickened ventral margin bears the pleural articular process of the middle coxa. The link plates between the mesothorax and the metathorax have their anterior attachments ventrally on the posterior part of the mesopleuron at the base of the inner surface of the flange (pl. 7 J; pl. 8 B, C, *2lpl*). In the conjunctival membrane just below each link plate is the second thoracic spiracle (pl. 7 J, L; pl. 8 B, *2Sp*).

On the inner surface of the mesopleuron there is never present a typical pleural ridge; but in most fleas the site of the usual ridge is occupied by a vertical bar that is entirely free from the pleural surface except for a dorsal connection on the upper margin and a ventral connection at the coxal articulation (pl. 8 B, C, D, *PlR*). The end connections of this pleural bar leave little doubt that the bar itself is the pleural ridge secondarily detached from the pleuron except at its extremities. A partial detachment of the ridge occurs also in the honey bee. In *Pulex* the pleural bar is absent, but evidence of its former presence remains in the form of dorsal and ventral thickenings of the pleuron. According to Wagner (1939) a free pleural ridge is present in the mesopleuron of all fleas except Sarcopsyllidae, Pulicinae, and the genus Corypsylla.

The pleura of the mesothorax have usually only narrow membranous connections with the notum, but in *Dactylopsylla, Opisodasys,* and probably related genera, an internal peglike process from an anterior thickening of the lower tergal margin is secured in a pit of the pleuron on the upper end of the pleural ridge (pl. 8 E, *o*). The peg can be pulled out of its socket, but normally it holds the adjoining plates together, and its flexibility allows a slight posterior flexion of the pleuron on the notum.

The sternum of the mesothorax is anchor-shaped as seen from below (pl. 8 G, J, S_2), the anterior part being widely expanded and the posterior part reduced to a narrow bar extending backward in the body-wall membrane between the coxae. The lateral wings of the anterior expansion are united with the lower angles of the pleura, the apparent lines of union being usually distinct (pl. 7 J, K, L, M), though in some cases the sternal wings appear as mere thickenings of the pleural margins (O, P), or they merge completely into the pleura (N). In side view, the anterior part of the sternum appears as a prominent lobe projecting over the bases of the middle coxae (J, L, N, P). The sternum is traversed by a median groove, from which is inflected a strong median plate that gives added support and rigidity to the horizontal intercoxal arm. The latter carries the mesal articulations of the coxae (pl. 8 H, J), to be described later, and from its posterior end gives off a pair of large, apodemal arms (G, H, J, *SAp*) that project upward and backward, and unite at their ends in a vertical plate (I). The elongate foramen enclosed by the apodemal arms gives passage to the nerve connectives between the mesothoracic and metathoracic ganglia (I, *nvp*).

The metathorax.—When the flea jumps, it is the metathorax that sustains the principal upward and forward thrust of the legs against the body, since the large hind legs unquestionably furnish the principal leaping force. The metathorax of the Siphonaptera, therefore, in striking contrast to that of the Diptera, is highly developed, and moreover is specially fitted for the part it plays in relation to the jumping mechanism. The notum is strengthened by a system of internal ridges, the pleura are braced by well-developed pleural ridges, the thin outer walls of the coxae are fortified by linear inflections in line with the pleural braces. These internal thickenings of the skeleton are always conspicuous in cleared whole specimens as strong dark lines, and are therefore appropriately shown in illustrations of the external surface, though the true outer features are the grooves of inflections that form the ridges.

The metanotum (pl. 8 K, M, N, O, N_3) resembles the mesonotum in general shape and size, and is bordered posteriorly by a flange (K, *nf*) overlapping the first abdominal tergum (*IT*). The flange tapers downward on each side but widens again as it turns forward on the ventral margin of the notum, and forms here an extremely delicate transparent lobe that overlaps the pleuron.

The surface of the metanotum presents two transverse grooves, and, on the lower part of each side, a connecting longitudinal groove. The first transverse groove lies very close to the anterior margin of the notum and is the *antecostal sulcus* (pl. 8 N, *acs*); it forms internally a prephragma of the metathorax (pl. 8 L; pl. 9 A, E, H, I, K, *2Ph*). The metathoracic phragma is relatively small, compared with the phragma of the mesothorax, and is deeply emarginate below. In dipterous insects, or in insects with small hind wings, the second phragma is always transferred to the mesothorax; its solid connection with the metanotum in the fleas, a condition found among other holometabolous insects only in the Coleoptera, might be taken, therefore, as evidence that the progenitors of the fleas were not derived from a long-established group of two-winged insects.

The second transverse sulcus of the metanotum lies near the posterior notal margin (pl. 8 N, *ns*), and forms internally a strong transverse *notal ridge* (pl. 9 A, C, D, H, I, K, *NR*). This ridge of the metanotum is termed a "posterior phragma" of the metathorax by Wagner (1939), but it is distinctly not marginal and lies well within the metathoracic haemocoele (pl. 9 A, C, *NR*). In some cases the true posterior margin of the metanotum is marked by a much narrower ridge (*u*) at the base of the flange (*nf*). The notal ridge (*NR*) of the flea's metathorax is suggestive of that which in winged insects divides the wing-bearing notum into an anterior scutal region and a posterior scutellar region, but nothing gives assurance of any such identity.

Near its lower end the transverse notal ridge gives off anteriorly, along the horizontal lateral sulcus (pl. 8 N, *r*), a short, longitudinal *accessory ridge* (pl. 9 A, C, D, H, I, K, *r*), which goes to the anterior edge of the notum, where usually it blends into a marginal thickening continued around the ventral edge of the notal plate. The accessory ridge thus sets off a small, oval or quadrate ventrolateral area (*n*) of the metanotum adjoining the upper edge of the episternum (C, D, I, K, *Eps*). At the anterior end of the accessory ridge is articulated on the notal margin the posterior end of the link plate between the mesothorax and the metathorax (pl. 9 C, H, I, K, *2lpl*). On each of these second link plates is attached a relatively large, flat muscle arising on the upper part of the hind coxa (pl. 14 D, *70*).

The small but always conspicuous ventrolateral area of the metanotum below the accessory ridge (pl. 8 K-O; pl. 9 A, C, D, H, I, K, *n*) has been variously interpreted by flea specialists. Fox (1941), and Ewing and Fox (1943) regard it as an upper subdivision of the episternum. Wagner (1939) mistakes the true episternum for the "mesosternum," and designates the lower notal area as the "episternum," though he says the homology of the latter is not established; inconsistently he notes that the flange of the "metepisternum" is suggestive of a "rudimentary wing." There is no anatomical justification for such interpretations; the area in question is an integral part of the notal plate, as indicated by Crampton (1931, fig. 1). It bears a small but distinct marginal flange (pl. 9 B, *nf*) that overlaps the pleuron below it (pl. 8 K, *nf*), and which usually can be followed upward into the wider posterior flange of the dorsal part of the notum. In *Pulex* the ventral edge of this lower notal area (*n*) is united beneath the flange with the episternal margin (pl. 9 D), but in other fleas examined the two plates are separated by a narrow membranous junction (C, I, K).

The notal ridge of the metanotum is continued downward on each side into the region of the pleuron, and terminates in an oval expansion that overlaps and firmly clasps the upper end of the pleural ridge (pl. 9 C, H, I. J, *s*). Seen from the outside in cleared specimens this interlocking structure looks like a ball-and-socket joint for movement between the notum and the pleuron; but the two parts are so closely united that an effort to separate them always results in a break, leaving the head of the pleural ridge still in the grasp of the notal ridge. It is evident, therefore, that this apparent notopleural "articulation" of the metathorax is for the purpose of solid union along the line of the notal and pleural ridges, and is not for controlled movement. The flexibility of the united ridges allows the pleuron to be twisted somewhat on the notum, but permits of no swinging movement in a longitudinal plane. In *Opisodasys* the notopleural connection is so close that the notal ridge appears to be continuous into the pleural ridge (pl. 9 K).

In a cross section of the metathorax of a flea in which the angulation between the notum and the pleuron is relatively small, as in *Pulex,* the notal ridge (pl. 9 M, *NR*) is seen to form a strong arch over the back, with its lower ends firmly clasping the upper ends of the pleural ridges (*PlR*). The latter in turn rest on the upper ends of the lateral ridges of the coxae (*CxR*); and finally, the coxal ridges are braced against the trochanteral articulations. There is thus in the metathorax of fleas such as *Pulex* a strong, sclerotized arch extending from the trochanters over the back, evidently developed to resist the pull of the long, powerful depressor muscles of the legs (*63*) that arise on the notum and are inserted on the trochanters. The same arch serves also to withstand the upward thrust of the legs.

In other fleas, such as *Dactylopsylla* and *Opisodasys* (pl. 9 H, K), in which there is a pronounced posterior angulation between the notal ridge and the line of the pleurocoxal ridges, the notal ridge (*NR*) and its accessory branch (*r*) on each side form a Y-shaped brace on the notal plate, with its stalk surmounted on the pleural ridge (*PlR*).

The metapleuron of the fleas is remarkable for the great size of the epimeron, which in most species has invaded the region of the first abdominal segment and overlaps the second segment (pl. 8 K, N, O, *Epm*). The pleural ridge of the metapleuron is generally present in typical form (pl. 9 D, H, I, K, *PlR*), being continuously inflected from an external pleural sulcus, and never partially detached from the pleural wall as in the mesothorax. The episternal area of the pleuron is relatively small (pl. 8 K, M, N, O, *Eps*), its lower part is usually strengthened by a submarginal thickening, and its ventral anterior angle is united with the expanded anterior end of the sternum (L). The episternum gives attachment to the pleural branches of the depressor muscle of the trochanter (pl. 10 A, C, *63b, 63c*).

The metathoracic epimeron is typically a large plate with a wide posterior flange (pl. 8 K, N, O, *Epm*). It expands upward behind the metanotum, and usually downward in a lobe overlapping the base of the hind coxa. The metepimeron thus appears to occupy the lateral part of the first abdominal segment, which has no sclerotization of its own, while the first abdominal tergum (*IT*) is reduced to a relatively small plate lying above the two epimera. A more generalized condition is seen in *Hystrichopsylla* (pl. 8 M); here the upper edge of the epimeron lies below the metanotum, and only the epimeral flange projects beyond it (pl. 9 I).

The part of the haemocoele covered by each epimeral plate evidently belongs to the thorax because it contains thoracic leg muscles (pl. 9 H), and yet it contains also the tracheal trunk of the first abdominal spiracle (ISp), and the spiracle lies on the area of the epimeron (pl. 8 K, M, N, O, *ISp*). It is difficult to explain the anatomical confusion encountered here, except on the assumption that the spiracle has retained its primitive abdominal position, and has been enveloped by the expanding thoracic epimeron. The spiracle always lies just within the base of the epimeral flange. An apparent reason for the great size of the metathoracic epimeron is the presence of the large coxal muscle spread over much of the epimeral wall (pl. 9 H, *58*). In addition there is a small intra-epimeral muscle (*57*) behind the coxal muscle.

The metasternum (pl. 9 L, S_3) resembles the mesosternum. Its widened anterior part is united laterally with the pleural episterna (*Eps*), and usually there is no line of demarcation between the sternal and pleural areas. The intercoxal arm of the sternum carries the mesal articulations of the coxae (G, M, *q*), and posteriorly gives off a pair of apodemal processes (L, *SA*), but the latter are not united at their distal ends as in the mesothorax.

IV. THE LEGS

The structure and the musculature of the flea's legs have been well described and illustrated by Jacobson (1940) in *Ceratophyllus styx*

Roths., and the following description, based principally on *Hystrichopsylla gigas dippiei* Roths. and *Dactylopsylla bluei* (C. Fox), agrees closely with Jacobson's account.

The forelegs, being attached to the anterior ends of the horizontal propleura, hang from beneath the head. The constricted bases of the coxae (pl. 7 B), and their pivotal articulations on the pleura (C) give the first legs a greater degree of rotary movement than that allowed the other legs by their wider connections and double articulations on the body. The broad fore coxae are ordinarily held in a transverse plane, so that their anterior walls present together a wide shieldlike surface descending from the head behind the mouth parts (pl. 1 H; pl. 10 F). So striking is this aspect of the fore coxae that it suggests a functional significance; possibly the broad coxal shield clears a passage through the inner fur of the host, or presses down the hairs to make the skin accessible to the piercing stylets.

The musculature of the fore coxa is shown by Jacobson (1940) to include a pair of large antagonistic muscles arising on the propleuron, and a small muscle attached on the sternum. The trochanteral muscles, functionally the levator and depressor of the telopodite, arise in the base of the coxa except for a small branch of the depressor, which, Jacobson says, takes its origin on the "prosternum," though the writer would regard the region so designated a part of the pleuron. Notal branches of the depressor, so highly developed in connection with the other legs, are not present in the prothorax. The femoral, tibial, tarsal, and pretarsal musculature appears to be alike in all three legs.

The legs of the mesothorax and the metathorax are so nearly alike in their structure and musculature that a description of the hind leg will serve for both pairs, except for minor differences to be noted in the coxal musculature. The large flat coxae of these segments hang from the pleura with their broad surfaces outward but at slightly different angles, the middle coxae being somewhat oblique, the hind coxae more nearly parallel, to the vertical plane of the body. Each coxa has both a pleural and a sternal articulation. The pleural hinge is of the usual type of structure, consisting of an articular process at the lower end of the pleural ridge and a shallow acetabulum on the base of the coxa. The sternal articulation, on the other hand, is a peculiar feature of the fleas. The sclerotic mesal wall of the coxa is deeply emarginate above (pl. 8 H; pl. 9 G) leaving a wide membranous area between the coxa and the sternum. In this membrane is an oval or fusiform articular sclerite (*q*) with a strong median thickening that articulates at one end on the sternum and at the other in the angle of the coxal emargination. This structure pertains to the mesothoracic as well as to the metathoracic legs. The coxa may thus be said to be hinged on a transverse axis between the pleuron and the sternum, but the hinge is by no means a rigid one, since the flexible sternal articulation allows the coxa a considerable rotary movement on the pleural articulation.

The hind coxa is strengthened by a strong internal ridge on its outer wall (pl. 9 F, *CxR*) and a somewhat weaker ridge on its mesal wall (G, *p*). The lateral ridge begins at the pleural articulation and runs down to the distal part of the coxa, where it ends at the emargination on the posterior side just above the trochanter, but in confluence with an apical thickening of the coxa that supports the trochanteral articulations (pl. 9 M). The mesal ridge (G, *p*) begins above at the apex of the dorsal emargination of the inner coxal wall, and ends below in the apical thickening of the coxa (M, *p*).

The part of the flea's coxa posterior to the coxal ridges is usually regarded as a meron. Crampton (1931) calls it the "meron," and says "it is characteristic of the fleas to have a well developed meron in the metathoracic leg." The postcarinal part of the flea's coxa, however, has no anatomical identity with the meron of such insects as Mecoptera, Trichoptera, and Lepidoptera. A true coxal meron, defined according to its nature in these latter insects, is a ventral expansion of the basal area of the coxa on which the thoracic remotor muscles of the leg are attached, correlated with a lengthening of these muscles by extension into the body of the coxa, and is bounded by the displaced accompanying basicoxal ridge. The single remotor muscle of the flea's hind coxa retains its primitive position of attachment on the upper margin of the coxa (pl. 9 H, *58*). The coxal ridges of the flea are mere strengthening devices, and similar ridges occur in other insects.

The musculature of the hind coxa of the flea includes four thoracic muscles, one arising on the epimeron, the other three on the sternum. The epimeral muscle is a remotor of the coxa (pl. 10 A, B, *58*) ; it is a broad sheet of fibers occupying most of the haemocoelic surface of the epimeron (pl. 9 H, *58*), and is inserted on the upper margin of the coxa behind the pleural articulation. This muscle appears to be absent in the mesothorax; a small muscle arising in the upper part of the middle coxa, which Jacobson thinks is its mesothoracic representative, is attached dorsally on the second intersegmental link plate (pl. 14 D, *70*). Two of the sternocoxal muscles of the metathorax have broad insertions within the coxa, one anteriorly in the upper part of the coxa (pl. 10 B, *59*), the other posteriorly in the distal part (*60*); their fibers converge to narrow attachments on the sternum (S_3) close before and behind the head of the coxal articular sclerite. These muscles appear to be respectively a promotor and a remotor of the coxa, but probably, because of the flexibility of the sternal articulation, they give also a rotary movement to the coxa on the pleural articulation. The second muscle of this pair is said by Jacobson to be absent in the mesothorax. The third sternocoxal muscle is a very small bundle of fibers (pl. 10 B, *61*) arising between the other two, and inserted on the inner face of the mesal articular sclerite (*q*).

The short trochanter has a dicondylic coxal articulation of the usual type with a transverse hinge axis on the end of the coxa (pl. 9 M, *Tr*); it is attached to the femur by an oblique linear joint in the vertical plane of the leg (pl. 10 D) that permits to the femur only a slight movement of production and reduction (relative to the axis of the leg). The nature of the trochanterofemoral joint unifies the trochanter and femur for vertical movement, and the hinge of the trochanter on the coxa thus becomes the axis of levation and depression for the telopodite as a whole (i. e., the part of the leg beyond the coxa).

The principal leg muscles are those that pertain to the trochanter. Functionally these muscles are levators and depressors of the telopodite, since they impart no individual movement to the trochanter. The levators include a broad, fan-shaped group of fibers spread over much of the lateral wall of the coxa (pl. 10 A, B, C, *62a*), and a smaller group (B, C, *62b*) arising on the mesal wall; the two muscles have a common insertion on the trochanter behind the axis of the coxotrochanteral articulations. The depressor of the trochanter (i. e., of the telopodite) is the most powerful muscle of the leg, and undoubtedly is the principal source of the flea's jumping power. It is made up of one group of coxal fibers and three groups of thoracic fibers (pl. 10 A, C, *63*), all inserted on a long, thick tendon (C, *63t*) traversing the coxa to its attachment on the trochanter anterior to the coxotrochanteral hinge. The coxal fibers of the depressor (*63a*) arise anteriorly in the coxa and go directly, in parallel formation, to the side of the tendon. The thoracic fibers comprise three groups converging on the end of the depressor tendon. Two smaller groups arise on the episternum, one anteriorly (*63b*), the other (*63*c) against the pleural ridge. The third group of depressor fibers (*63*d) is the largest of all; it takes its origin dorsally on the metanotum (pl. 9 M, *63*) and pulls directly on the depressor tendon (*63t*).

The trochanter contains the usual small reductor muscle of the femur (pl. 10 B, E, *64*), which evidently is opposed by elasticity of the trochanterofemoral joint. The muscles that lie within the femur (D, E) are an extensor and a flexor of the tibia, and a femoral branch of the flexor of the pretarsal claws. The tibial muscles are large, flat, pinniform groups of fibers on axial tendons; the extensor lies against the mesal wall of the femur (E, *65*) and is attached by its tendon dorsally on the base of the tibia, the flexor fibers spread over the lateral wall of the femur (D, *66*) and their tendon is attached ventrally on the tibia.

The tarsal musculature consists of a pair of antagonistic muscles arising one (D, *68*) laterally, the other (E, *67*) mesally in the tibia, where their fibers are separated by an enlargement of the tibial trachea (E, *Tra*). These muscles appear to be inserted laterally and mesally on the tarsal base as if to give the tarsus a transverse movement (relative to its usual posteriorly extended position). In a living flea the tarsus is often so turned that the claws assume a horizontal position in order to grasp the vertical shaft of a hair, and in dead specimens the tarsi are very commonly twisted in this manner. Yet when a flea sits or walks on a smooth surface the claws are turned downward. The long curved claws usually have a prominent basal lobe (H, I) forming a deep notch on the under surface, in which a hair may become firmly lodged. It is interesting to note the similarity of the flea's claws to the claws of the parasitic Hippoboscidae and Nycteribiidae among the Diptera. In *Echidnophaga,* however, the claws are simple (G). Proximal to the claws, on the under surface of the pretarsal segment, is a typical, partly invaginated unguitractor plate (H, *Utr*), on which is attached the tendon (*69t*) of the flexor muscle of the claws. One group of fibers of this muscle arises in the upper part of the tibia (E, *69a*), the other in the base of of the femur (D, *69*b).

When a flea is at rest the femora are turned upward on the coxae and the tibiae downward on the femora, so that the legs are flexed at the two principal joints and thus always ready for extension. In walking or running on an unobstructed surface the flea uses the three pairs of legs equally as do other insects, but among hairs or cotton fibers the middle and hind legs serve for propulsion while the forelegs are moved wildly about in all directions to find and seize the nearest support. When the flea jumps, the leap is so instantaneous that the leg action cannot be observed, but apparently the insect simply straightens the legs without crouching or making any other preliminary movement.

Jacobson (1940) points out that the jumping mechanism of the flea differs from that of the saltatorial Orthoptera in that the leap is effected principally by the downward flexion of the femora, rather than by the extension of the tibiae. The size of the leg-depressor muscles attached on the trochanters can leave little doubt that the action of the femora is most important, but the size of the femora themselves and of the tibial muscles they contain would indicate that the extension of the tibiae plays also an important part in the spring. Propably the leap is effected by a simultaneous extension of both the femora and the tibiae, and thus acquires its extraordinary force. The hind legs undoubtedly are the principal jumping organs, but the similarly developed and strongly musculated middle legs must be effective accessories.

The inner surfaces of the hind coxae of some fleas are armed near their lower ends each with one, two, or several horizontal or oblique rows of small but strong spines. Enderlein (1929) records having observed fleas with the abdomen elevated vigorously rubbing the hind coxae over the ridged lateral surfaces of the large second abdominal sternum. The leg movement was so regular and continuous that it could not be regarded as a cleaning act, and Enderlein, therefore, contends that the coxal spines and abdominal ridges constitute a sound-producing apparatus, though the sound supposedly produced is not audible to the human ear.

V. THE ABDOMEN

The abdomen of the adult flea includes 10 segments; only 10 abdominal segments are present in the larva (fig. 3), and also in the pupa (fig. 6 A). According to Kessel (1939), 11 segments are found in the abdominal region of the young flea embryo, but the eleventh segment soon disappears by invagination with the proctodaeum. Wagner (1932), by an involved argument, has attempted to show that 12 segments enter into the formation of the adult abdomen of the flea, but, in the face of the visible facts, his conclusions seem far-fetched and entirely unnecessary. Holometabolous insects in general have only 10 abdominal segments; if there is any remnant of an eleventh segment it is represented by an invagination at the end of the tenth segment containing the true anal opening of the proctodaeum. The eleventh abdominal segment is distinctly present in most orthopteroid and apterygote insects, but the only hexapods known to have 12 abdominal segments in the adult stage are the Protura.

Abdominal segments *I* to *VII* may be designated pregenital segments. Segment *VIII* is the genital segment of the female, segment *IX* that of the male, but in each sex the plates of both these segments are modified in connection with the reproductive functions. Segment *X* forms a conical endpiece of the abdomen; on the anterior part of its dorsum is the specialized sensory area known as the *pygidium,* at its apex is the anus.

The pregenital segments.—Segments *I* to *VII,* inclusive, of the flea (pl. 11 A, B) are typical abdominal segments in that they are separated by ample, infolded membranous conjunctivae, and each segment but the first is covered by a tergal and a sternal plate overlapping on the sides. The parts of the terga and sterna that are in contact with the haemocoele, however, are relatively small (pl. 11 C, E, G, H, I, J, L, N); in each plate the posterior limit of the haemocoelic area is defined by the externally visible line (*v*) on which arises the conjunctiva to the next segment. The part beyond this line is a thin, transparent solid extension of the segmental plate that constitutes a free flange (*f*). The flange covers much of the succeeding tergal or sternal plate, and extends far downward from the sides of each tergum and upward from each sternum. The broadly overlapping dorsal and lateral parts of the terga and sterna, therefore, are the flanges.

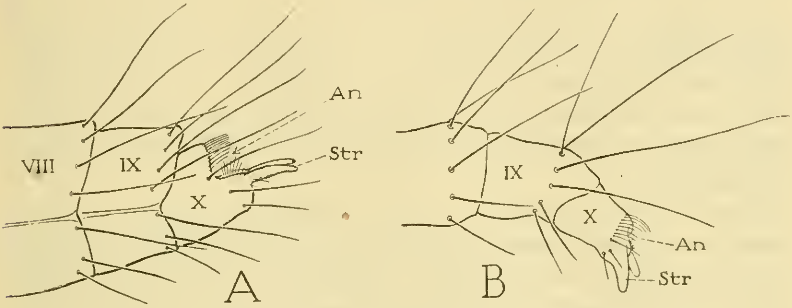

FIG. 3.—Terminal segments of two species of flea larvae.

A, *Cediopsylla simplex* (Baker), from rabbit nest. B, unidentified species from nest of pack rat.

An, anus; *Str,* anal struts.

The large setae so characteristic of the flea's abdomen arise mostly from the haemocoelic areas of the segmental plates, and wherever setae are on the areas of the flanges, the flange is penetrated to the setal bases by extensions of the haemocoele (pl. 11 M). Even the spines of abdominal ctenidia on the margins of the flanges (G, H) have at their bases what appear to be remnants of haemocoelic canals (F). The setal patterns of various abdominal segments are shown in the figures of plate 11. A few fleas have well-developed abdominal ctenidia on the terga of the first three or first six segments; in others the spines may be present, much reduced in size and numbers, and limited to the first four terga, or to the second, third, and fourth (pl. 11 A).

The first abdominal segment has a tergal plate only (pl. 11 A, B, *IT*), which is relatively small and covers only the upper part of the dorsum. The rest of the first segment not invaded by the metathoracic epimera is membranous.

The second segment is characterized by the large size of the sternum (pl. 11 A, B, *IIS*), and by the wide overlapping of the sternum against the lower parts of the tergum of its own segment (*IIT*) and the tergum of the following segment. The broad, winglike expansions of sternum *II* (D) thus clasp the sides of the base of the abdomen, and appear to give a ventral support to the abdomen on the thorax.

The third, fourth, fifth, and sixth abdominal segments have no special structural features (pl. 11 A, B). The setae are repeated in similar pattern from segment to segment, and the broad tergal flanges widely overlap the flanges of the respective sterna along the sides of the abdomen. Lateral spots sometimes seen on the sterna of these segments and also on the second sternum (pl. 11 A) mark the attachments of transverse intrasternal muscles.

The seventh segment in general resembles the segments preceding it (pl. 11 A, B), though the sternum may be much enlarged and extended backward so far as to cover the eighth sternum (A, *VIIS*). In the male the plates of this segment overlap in the usual manner (A), but in the female the seventh sternum overlaps the lower edges of its tergum (pl. 1 A, C, F, G; pl. 11 B, *VIIS*). In *Pulex irritans* the posterior border of the seventh sternum contains a notch (pl. 1 A; pl. 11 K), which probably has some relation to the use of the genital claspers by the male. A common feature of the seventh tergum in both sexes is the presence of one or several pairs of long *antepygidial setae* projecting prominently on the back from the rear margin of the tergal flange (pl. 11 A, B, J, L, N). Each lateral group of these setae is usually set on a small elevation of the flange margin, and is accompanied by a broad extension of the haemocoele into the flange (M). In the pupa the seventh tergum bears a pair of antepygidial lobes (pl. 13 N, O, *apl*), within which the long setae of the imago attain their length before emergence.

The eighth abdominal segment.—The tergal and the sternal plates of segment *VIII* are always different in the two sexes of the same species, though in some species they approach similarity. In the female flea the plates of the eighth segment are essentially constant in form, but in the male there is much variation in the relative size and shape of both the tergum and the sternum. The spiracles of this segment lie in the lower ends of setigerous grooves, which usually are confined to the posterior margins of the tergum at the sides of the pygidium (pl. 12 C, D, E; pl. 15 B, *Sp*).

The eighth segment of the female flea differs from the segments preceding it in the great size of the tergum as compared with the sternum (pl. 1 A, F; pl. 12 A, *VIIIT, VIIIS*); in most cases the small sternum is not visible in a lateral view of the whole insect. The tergum consists usually of two lateral plates, narrowed dorsally (pl. 11 B; pl. 12 B, *VIIIT*), separated on the midline of the back (pl. 15 B), and expanded on the sides as two large valvelike, bristly lobes with free posterior and ventral margins. The eighth sternum of the female is a very small, oval or elongate, weakly sclerotized plate, lying between the lower margins of the tergal lobes and more or less concealed by the latter (pl. 12 B; pl. 15 B, *VIIIS*).

In the male flea the eighth segment in some species resembles that of the female in the relative size of the tergum and sternum, while in others the size relation of the plates is reversed. In such fleas as *Pulex, Ctenocephalides,* and *Echidnophaga,* the tergum of segment *VIII* in the male is a small plate occupying only the upper part of the segment (pl. 1 B, D; pl. 12 C, *VIIIT*); the sternum (*VIIIS*), on the other hand, is so large that it covers the sides and the venter of the segment, its expanded lateral parts being continuous below from one side to the other. In these fleas, therefore, the sternum of segment VIII in the male occupies the areas covered by the expanded lateral parts of the eighth tergum in the female (cf. A and B of pl. 1). In *Pulex* and *Ctenocephalides* the lower edges of the eighth tergum are slightly overlapped by the upper angles of the sternum (pl. 12 C); the thickened lower edge of the tergum of *Pulex irritans* is produced anteriorly in a small tergal apodeme (E, *ap*).

In most other male fleas the sternum of the eighth segment becomes reduced in size and takes on highly specialized forms, while the tergum either remains small or becomes greatly enlarged. In *Hystrichopsylla* tergum *VIII* (pl. 12 G; pl. 16 B) resembles that of *Pulex* or *Ctenocephalides,* but the sternum is a V-shaped plate with ascending arms reaching up to the tergum (pl. 16 B), and the apex produced into a pair of broad posterior arms (pl. 12 F, G), which closely embrace the median lobe of sternum *IX*.

Corresponding with the reduction of the sternum in the male eighth segment, the eighth tergum in some groups of fleas becomes greatly enlarged by a ventral expansion of its lateral parts. An example of this type of structure is here shown in *Dactylopsylla bluei* (C. Fox) (pl. 12 D). The dorsally separated lateral halves of the tergum (*VIIIT*) in this species extend far down on the sides of the abdomen and expand below the spiracles into a pair of large, valvelike plates embracing the genitalia. Here, therefore, in the male, the tergal plates of segment *VIII* have the relative size and form of the eighth tergum characteristic of female fleas. The eighth sternum of *Dactylopsylla bluei* is a fairly large bilobed plate (pl. 12 D, *VIIIS*, I), but in other species it is usually smaller, and takes on various shapes, particularly diversified in the form of the apical lobes (pl. 12 H, J, K; pl. 13 A, D). Other forms assumed by the plates of segment *VIII* in male fleas are described and illustrated by Wagner (1932).

In certain fleas the intersegmental membrane between the eighth and ninth sterna of the male is produced into lobes of various shapes. An example of a simple structure of this kind is seen in *Ceratophyllus swansoni* Liu (pl. 13 A, *w*); in *Opisodasys pseudarctomys* (Baker) a corresponding pair of large, soft, expanded lobes covered with short setae arises behind the very small eighth sternum (pl. 12 J, *w*). Wagner (1939) observes that these intersegmental lobes in Ceratophyllinae appear to have some relation to a special organ near the base of the eighth sternum, having an oval cavity with numerous internal outgrowths. This organ Wagner believes is a gland which spreads its secretion on the intersegmental lobe, and probably has some functional role in mating.

The ninth abdominal segment.—Segment *IX* is highly modified in the male; in most female fleas it is practically obliterated. Well-developed ninth-segment plates, however, are said by Wagner (1932, 1939) to be present in the females of *Ctenophthalmus*, Rhadinopsyllinae, *Hystrichopsylla*, and *Parapsylla*, which were first observed, but not identified with the ninth segment, by Rothschild in *Ctenophthalmus agyrtes* Hell.

The plates of the female ninth segment in *Hystrichopsylla gigas dippiei* Roths. are readily exposed by removing the overlapping plates of segment *VIII*. There is then to be seen in the membranous wall of the abdomen proximal to segment *X* (pl. 12 L, M) a pair of large, elongate lateral sclerites (*IXT*) lying close to the sides of the pygidial plate, but entirely separate from the latter. These two ninth-segment plates are widely separated on the dorsum, but ventrally they come together beneath the subanal lobe of segment *X*. Wagner (1932) shows the presence of a similar pair of lateral plates in *H. talpae* (Curtis), but in addition he finds a pair of weakly sclerotized ventral plates between their lower ends, which he regards as sternal sclerites. In *Ctenophthalmus,* he says, there are two plates on each side, one dorsal, the other ventral, but in other forms only a single dorsal plate is present (see Wagner, 1932, figs. 6 and 9). Wagner cites evidence from which he concludes that in female fleas having no distinct ninth-segment sclerites the tergal plates of segment *IX* have united with the pygidial plate, and may in some cases take the form of lateral lobes of the latter, as in *Chaetopsylla trichosa* Kohaut and in *Vermipsylla alacurt* Schimk. (Wagner, 1932, fig. 9).

In male fleas the tergum of the ninth segment is variable in size, always small, and may be reduced to the point of obliteration. Its anterior margin is usually produced into an apodemal inflection beneath tergum *VIII*. The tergal apodeme takes the form of a narrow band, a pair of phragmalike lobes, or a broad plate much larger than the supporting tergum itself.

The ninth tergum in the males of *Ctenocephalides, Pulex,* and *Echidnophaga* is a narrow sclerite arched over the back at the base of the pygidium (pl. 17 A, E, H, *IXT*). Its lower, somewhat expanded ends extend downward below the pygidium, where they are weakly connected with the ascending arms of the ninth sternum (pl. 17 E, *IXS*). In *Ctenocephalides felis* the anterior tergal margin is extended on each side into a large apodemal lobe (A, *tAp*) ; in *Pulex irritans* (E) the lateral apodemal plates are separated dorsally by only a deep, medium notch, and are extended ventrally into the arms (manubria, *Mnb*) of the clasper lobes (*CL*) ; in *Echidnophaga gallinacea* (H) the apodeme is a wide plate continuous from one side to the other, and fused ventrally with the slender manubrial arms of the claspers.

A different type of structure in the tergal region of segment *IX* is well illustrated in the male of *Hystrichopsylla* (pl. 16 C, D, H). Here a narrow but distinct tergal plate (*IXT*) is continuous at its lower ends with the upper basal angles of the large clasper lobes (*CL*), and appears as a mere yoke by which the claspers are suspended from the back. The tergal apodeme in *H. gigas dippiei* is very small (C, H, *tAp*), being simply a short inflection of the tergal margin beneath the conjunctiva from tergum *VIII*.

The intimate union of the ninth abdominal tergum of the male with the clasper lobes, plainly seen in *Hystrichopsylla,* is a feature characteristic of the majority of the fleas, but in most such species the tergum itself becomes reduced to a narrow strip over the back (pl. 17 K, *IXT*), or more commonly to a mere line on which are attached the conjunctiva from tergum *VIII* and that to segment *X* (pl. 17 J, L, M; pl. 18 B, *IXT*). In most such cases the tergal apodeme (*tAp*) is relatively large and is broadly united with the bases of the clasper arms (*Mnb*). The basal lobes of the genital claspers (*CL*) thus come to have the appearance of being extensions of the ninth tergal apodeme, and some students of fleas have mistaken the apodeme for the tergum. The true explanation of the anomalous condition presented here is given by Wagner (1932).

The ninth sternum of the male is characteristically V-shaped, with the ventral apex extended posteriorly in a medium arm (pl. 12 N, O, P), which is usually branched into a pair of apical lobes (pl. 13 A, B, C, D) that take on various forms. The ascending arms of the sternal V usually reach up to the lower ends of the ninth tergum (pl. 16 C; pl. 17 E), and their upper parts embrace the bases of the genital claspers (*CL*); between their lower parts is an invagination of the body wall that forms a pocket (pl. 17 E, *aedP*) from which arises the aedeagus. An apodemal rod always associated with the internal sack of the intromittent apparatus (fig. 5, *aprd*) arises in some genera in the crotch of the ninth sternum from the dorsal wall of the median arm of the latter (pl. 12 R; pl. 13 A, B, C, D).

The tenth abdominal segment.—The abdomen of the flea terminates with a small, asymmetrically conical body (pl. 12 L, *SegX*) having a declivous dorsal surface exposed between the lateral plates of the eighth segment (pl. 11 A, B; pl. 12 A), and a relatively short ventral surface (pl. 12 L), which is ordinarily concealed. This apical body of the flea's abdomen is segment *X*. The broad anterior part of its dorsum is mostly occupied by the so-called *pygidium* (pl. 12 M; pl. 13 E-I, K, P, *Pyg*); the distal part culminates in an anus-bearing cone, which may be termed specifically the *proctiger* (pl. 13 F, G, I, *Ptgr*). In the female a pair of short, bristle-bearing *anal stylets* arises dorsally at the base of the proctiger (pl. 12 M; pl. 13 E, H, K, P, *astl*). The entire tenth segment of the female is embraced by the sclerites of the ninth segment in female fleas, such as *Hystrichopsylla*, that have a sclerotized ninth segment (pl. 12 L, M); in all male fleas, however, though the pygidial area of the tenth segment lies close against the ninth tergum (pl. 13 F), the sternum of the ninth segment is far removed from the proctiger (fig. 5, *IXS*), and in this sex a long intersegmental membranous area extends down from the short subanal surface of the proctiger into the dorsal wall of the aedeagal pocket (*aedP*), whence it is reflected back to the sternum.

The structure called the pygidium in the fleas is a well-defined area of the dorsum of the tenth segment, irregularly quadrate, oval, or reniform in shape, and varying much in relative size in different species. Its surface is densely clothed with small setae or spicules, and supports from 20 to 40 long slender hairs deeply set into strongly ribbed sockets. The structure of the pygidium, particularly of the hair sockets, is described by Lundblad (1927), who terms the hair organs trichobothria, but gives nothing of their nerve connections or of the cellular matrix beneath them. The hairs would appear to be receptive elements of sensory organs, and it might be supposed that they respond to atmospheric disturbances, perhaps to sound, but the writer knows of no experimental evidence of their function; "tickling" the pygidium of a feeding flea elicits no response on the part of the insect.

The term "pygidium" (little rump), when used in entomology, generally applies to the entire dorsum of the tenth abdominal segment. The organ called the pygidium in the fleas, therefore, was probably so named with the idea that it alone represents the tergum of segment *X*, the proctiger being referred to an eleventh segment. Since, however, there is no evidence of segmentation in the pygidio-proctiger region, the flea pygidium must be regarded as merely a differentiated sensory area of the dorsum of the tenth abdominal segment.

The pygidium is often framed in a well-defined plate (pl. 13 E, F, H), which in the female (E, H) is continuous into the dorsal lobe of the proctiger. In the male the pygidial plate usually ends at the base of the proctiger (F), and the latter may be distinctly set off by a groove or membranous area from the region of the pygidium (I, L), thus giving the proctiger the appearance of being a distinct segment. Just behind the pygidium there is usually to be seen in the pygidial plate a pair of transverse grooves (pl. 13 F, G, *acs*), which form postpygidial apodemal ridges or processes on the inner surface (L, *ppgAp*). In *Echidnophaga gallinacea* a single, strong, postpygidial apodemal ridge (J, *Ac*) is continuous from one side to the other. In the male flea there are attached on the postpygidial apodemes or ridge two broad bands of muscle fibers diverging posteriorly from the ninth tergum or its apodeme (J, *71*). These fibers are evidently the intersegmental dorsal muscles between segments *IX* and *X*, which, in the generalized structure of the abdomen (fig. 4 A, *dmcl*), are attached posteriorly on the antecosta of the tenth tergum (*XAc*). The attachment of these muscles in the flea on apodemal processes or a ridge behind the pygidium (fig. 4 B), therefore, is evidence that the pygidial plate (*Pyg*) is merely an enlargement of the precostal area of a simple tergum (A, *Prc*), accommodating the development of the sensory organ on it. The dorsal pygidial muscles are not present in female fleas, perhaps for

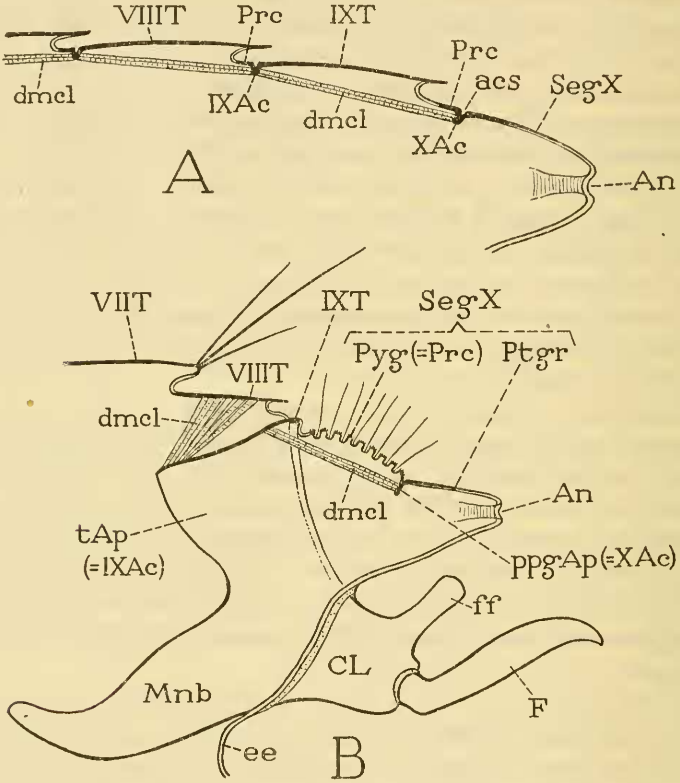

Fig. 4.—Diagrams showing the relation of the structural modifications in the ninth and tenth abdominal segments of a male flea to the generalized structure of segmental plates.

A, generalized structure and relation of successive tergal plates, in which the intersegmental dorsal muscles are attached on submarginal antecostae of the terga. B, typical structure of the eighth and ninth abdominal terga and the tenth segment of a male flea, showing the relation of the clasper and manubrium to the ninth tergum.

Ac, antecosta; *acs*, antecostal sulcus; *An*, anus; *CL*, clasper lobe; *dmcl*, intersegmental dorsal muscles; *ee*, inner wall of aedeagal pouch; *F*, movable finger of clasper; *ff*, process of clasper lobe; *IXAc*, antecosta of tergum *IX*; *Mnb*, manubrium; *ppgAp*, postpygidial apodeme; *Prc*, precostal area of tergum; *Pyg*, pygidial sense organ; *SegX*, tenth segment; *T*, tergum; *tAp*, apodeme of tergum *IX*; *XAc*, antecosta of tergum *X*.

the reason that few female fleas have ninth-tergal plates, but other muscles from some ventral source are attached on the postpygidial apodemes in each sex.

The segmental unity of the pygidio-proctiger region is evident in a flea pupa (fig. 6 A, *X*; pl. 13 N, O, *SegX*), in which there is no suggestion of separate pygidial and anal segments. In a female pupa the anal stylets (pl. 13 N, O, *astl*) arise just above the anal region, which is marked by a median depression but has not yet developed the dorsal and ventral anal lobes of the imago, seen within the pupal skin at N. The anal stylets have been regarded as cerci by some students of fleas, but true cerci belong to the eleventh abdominal segment. Wagner (1932), in an attempt to make out 12 segments in the abdomen of the flea, and to identify the stylets with cerci, has postulated that the stylets belong to the venter of an eleventh segment, which, in the female, has invaded the dorsum between the pygidium and the proctiger. Sharif (1937), however, says the anal stylets of the rat flea "are formed as a pair of finger-like evaginations of the thickened ectoderm on the dorso-lateral sides of the tenth abdominal tergum of the female prepupa."

The terminal appendages, or "anal struts," of the flea larva (fig. 3, *Str*) have no relation to the anal stylets of the imago. According to Sharif (1937) "these structures are only retained up to the pupal stage and disappear in the adult." The "anal struts" of the flea larva superficially resemble the anal prolegs, or pygopods, of other holometabolous larvae.

In some fleas a pair of lateral lobes projects from the tenth segment behind the pygidial plate, as seen in *Opisodasys pseudarctomys* (pl. 13 K, *z*). Wagner (1932) gives a comparative account of these structures which are usually soft, hair-covered or spiny lobes; in *Neopsylla,* he says, they are partly united with the surface of the proctiger, in *Ischnopsylla elongatus* they take the form of strong, hornlike processes.

The proctiger usually appears to be divided by the anal cleft into a dorsal lobe and a ventral lobe, each of which may contain a distinct plate (pl. 12 L, M; pl. 13 E, K; pl. 17 A, L, M), but the lateral extent of the cleft is variable, and in some cases the dorsal and ventral plates are entirely united laterally by menbranes (pl. 13 G). Both lobes are usually simple, with rounded or tapering margins, but the ventral lobe is sometimes cut into a pair of lateral processes (pl. 17 K, *val*) or divided into long tapering arms (pl. 13 M; pl. 18 A, *val*). The proctiger of the flea, however, never has the structure typical of a persisting eleventh segment, in which the anus is enclosed by a dorsal *epiproct* and a pair of ventrolateral *paraprocts*. These terms, therefore, are not applicable to the anal lobes or plates of the Siphonaptera, or to those of any other insect in which the eleventh segment has been eliminated.

In the males of some fleas the subanal plate of the proctiger is supported by basal extensions or a pair of lateral sclerites lying close beneath the edges of the pygidial plate or attached to the latter (pl. 13 G; pl. 17 J, M, *x*). These sclerotizations are termed "subanal sclerites" by Wagner (1932), who would interpret them as sternal remnants of an eleventh segment supposedly interpolated between a tenth pygidial segment and a twelfth anal segment. The ventral sclerites of the male, Wagner contends, represent corresponding sclerites of the female that have been transposed to the dorsum, where they bear the anal stylets, which latter are thus shown to be true cerci. This type of reasoning is hardly to be recommended for general use in morphology, and in the present instance it gives results entirely refuted by the segmentation of the larva and pupa of the flea, and unsubstantiated by the anatomy of the adult insect.

VI. THE SPIRACLES

Most fleas have the usual 10 pairs of spiracles, 2 of which are thoracic, and 8 abdominal. The females of *Tunga penetrans* (L.), however, have only five pairs of spiracles on the abdomen, which pertain to segments *I, V, VI, VII,* and *VIII,* but, as if to compensate for the missing spiracles, the last four on each side are exceptionally large. In the larval flea the first spiracles are on the sides of the prothorax, the second on the metathorax, the post-thoracic spiracles on segments *I* to *VIII* of the abdomen. In the adult, the two pairs of thoracic spiracles are intersegmental in position, being in the conjunctivae between the prothorax and the mesothorax, and between the mesothorax and the metathorax; the first abdominal spiracles lie in the expanded metathoracic epimera; the other seven abdominal spiracles are on the terga of their respective abdominal segments. As with adult insects in general, the thoracic spiracles of the fleas differ in structure from the abdominal spiracles.

The first thoracic spiracles.—The first spiracles of the thorax in the adult flea are contained in the intersegmental plates that link the mesothorax with the prothorax (pl. 7 L, P; pl. 8 A, 1*Sp*). The trachea of each spiracle penetrates a shallow cavity on the inner surface of the plate (pl. 14 B, C, *Tra*), and opens by a minute orifice in a small membranous area on the outer surface (A). An occlusor muscle arising within the cavity of the plate (C, *mcl*) is inserted on the membrane; its contraction evidently draws in the membrane and constricts the spiracular aperture.

The second thoracic spiracles.—The second spiracles of the thorax are closely associated with the link plates between the mesothorax and the metathorax, but are not contained in them; they lie in the conjunctival membranes just below the plates (pl. 7 J; pl. 8 M, N, O; pl. 14 D, E, G, *2Sp*). Each spiracle of this pair may be simply the tracheal aperture surrounded by a thickened rim, but the spiracle is usually elevated or borne on the summit of a small papilla. The papilla is particularly large and prominent in *Ctenocephalides,* in which it is usually to be seen projecting above the coxa from beneath the posterior angulation of the mesopleuron (pl. 7 L, *2Sp*). The conical papilla of *C. felis* (Bouché) arises from an oval basal plate in the conjunctival membrane, which is perforated by a foramen that admits the trachea (pl. 8 B, *2Sp*). The soft walls of the papilla are strengthened by a framework supported on the basal plate (pl. 14 H), and the delicate apical section tapers to a small thin lobe, at the side of which is a funnel-shaped depression that contains the tracheal aperture (ostium spiraculi, *Osp*). A small muscle (*mcl*) arising ventrally in the papilla is inserted at the distal end of the trachea. According to Wigglesworth (1935), "when this muscle contracts the trachea is drawn inwards and the soft tip of the papilla occludes the external opening." A more simple but similar structure of the spiracular papilla is seen in *Hystrichopsylla* (pl. 14 F).

The abdominal spiracles.—The spiracles of the abdomen differ consistently from the thoracic spiracles in the structure of their closing apparatus. Moreover, instead of being flush with the body surface or elevated on papillae, the abdominal spiracles are sunken into cuticular pits or grooves of the body wall (pl. 14 I, L, M, O, Q, *fs*). These external spiracular fossae are commonly mistaken for the spiracles themselves, but the true ostium of the spiracle (*Osp*) lies anteriorly or ventrally in the fossa (*fs*), where usually it is guarded by slender spines arising from the walls of the latter. The ostium leads into a short tubular or bottle-shaped atrium (*Atr*), the walls of which are strongly ringed, but the atrial rings are generally thicker than the taenidia of a trachea. The atrium is connected with its trachea (*Tra*) by a thin-walled section of the respiratory passage, constricted like an hourglass at its middle and devoid of rings. The constriction is embraced by the closing apparatus (pl. 14 J, L, N, O, P, Q, R). The latter consists of a bow-shaped rod on one side of the respiratory tube (J, L, N, P, *rd*), and of a muscle on the other side (J, O, *mcl*) stretched between the two ends of the rod. Wigglesworth (1935) shows in a sectional view (pl. 14 K) that the narrow part of the air tube (*Tra*) runs through a deep notch on the concave side of the rod (*rd*). Consequently, when the muscle contracts, the respiratory passage is pinched and the tracheal entrance is thereby closed.

The spiracular closing apparatus of the adult flea appears to have no relation to that of the larva, which, as described by Sharif (1937), has a quite different structure. The atrium of an abdominal larval spiracle, Sharif says, has an internal fold just before the tracheal entrance; a small muscle arising on the body wall runs parallel with the atrium to attach on the end of the trachea. Contraction of the muscle causes the atrial fold to occlude the mouth of the trachea.

The first abdominal spiracles, which in the larva lie on the sides of the first abdominal segment in line with the other spiracles, are taken over in the adult by the metathoracic epimera, which have invaded the lateral areas of the first abdominal segment. The position of these spiracles on the epimera differs in different species of fleas, but the spiracular pit either lies directly over the haemocoele beneath the epimeron (pl. 9 A, *1Sp*), or, if it is on the region of the epimeral flange (I), it is accompanied by an extension of the haemocoele into the flange (pl. 14 M). Some writers refer to the epimeral spiracles of the adult as "the third thoracic spiracles," but the facts that these spiracles have the structure of abdominal spiracles, and that the corresponding spiracles of the larva are on the first abdominal segment, leave no doubt of their abdominal origin. No other pterygote insect has three pairs of spiracles on the thorax.

The following six pairs of spiracles are situated on the lateral parts of the tergal plates of their respective segments, always within the haemocoelic area of the tergum (pl. 11 C, G, H, J, L, N, *Sp*). Owing to this position, each spiracle is usually covered by the flange of the preceding segment.

The spiracles of the eighth abdominal segment lie in the lower ends of deep setigerous grooves on the posterior margins of the eighth tergum at the base of the pygidium (pl. 12 C, E; pl. 15 B, *fs*). In the lower end of the elongate fossa is a depression similar to the pits of the preceding spiracles, which contains the true spiracular ostium (pl. 14 N, O, *Osp*) that leads into the atrium (*Atr*). The ventral pit of the fossa is sometimes so deep as to form a distinct entrance chamber to the spiracle from the open part of the fossa (Q), and in some fleas a long tubular extension of the fossa, with the spiracle at its lower end, goes far down in the side of the tergum (R, *fs*).

In his experimental study on the respiration of *Xenopsylla* *cheopsis* Roths., Wigglesworth (1935) describes the action of the spiracles in the living flea, and the regulation of respiration by differences of oxygen and carbon dioxide content of the air, by metabolites in the blood, and by temperature. Tracheal pulsations in the flea (*Archaeopsylla erinacei*) are noted and discussed by Herford (1938), who says "the tracheal rhythm is one of slow collapse of the main tracheal trunks, followed by a sudden inflation." When fully inflated the tracheae are thrown into curves and loops; on deflation these irregularities shorten and straighten, and the walls of the larger trunks collapse. During deflation most of the spiracles are closed and the liquid in the tracheoles slowly rises, suggesting that deflation of the tracheae results from the absorption of oxygen. On the opening of the spiracles the tracheae expand, presumably by their own elasticity, and the liquid in the tracheoles retreats. The flea makes no perceptible muscular movements of respiration.

VII. THE FEMALE GENITALIA

The genital region of the female flea is enclosed by the lateral expansions of the large tergal plates of the eighth abdominal segment (pl. 15 A). Viewed from behind (B) there is seen below the proctiger a deep cavity (*GC*) between the valvelike tergal plates. This cavity is the *female genital chamber*. Its soft anterior wall has a smooth convex surface, the lateral margins of which are reflected into the inner walls of the enclosing tergal plates. The entrance to the chamber is guarded by long external setae of the tergal plates, and may be further protected by opposing rows of transverse setae on the inner margins of the plates. Ventrally the chamber is closed by the upturned eighth sternum (B, *VIIIS*), which has the appearance of a small median lobe between the lower edges of the tergal plates, but it is membranously attached along its sides to the latter, so that only its rounded apex forms a free margin.

By depressing the eighth sternum there is to be seen between it and the descending anterior wall of the genital chamber a deep, narrow pocket (pl. 15 C, *Vag*) that extends downward to the base of the eighth segment, where the median oviduct opens into its lower end (G, *Odc*). This pocket of the genital chamber is the *vagina* of the flea (the genital passage so called in female insects being always a differentiated part of the genital chamber). The distal vaginal opening, or gonotreme, above the end of the eighth sternum (B, *Gtr*) is the exit from which the eggs are discharged; the true *gonopore* is the mouth of the median oviduct at the inner end of the vagina

(D, G, *Gpr*). In the dorsal, or anterior, wall of the vagina is the aperture of the sperm-receiving organs (D-G, *Ob*), which, by way of a duct, leads immediately into a small sack called the *bursa copulatrix* (G, *Bcpx*). During mating, therefore, the male flea must gain entrance to the external genital chamber of the female, open the mouth of the vagina, and within the latter find the minute orifice of the sperm receptacle. Fertilization of the eggs takes place apparently by the discharge of sperm on each egg individually as it passes through the vagina.

The sperm receptacle of the female flea is said by Sharif (1937) to be formed in the prepupal stage as an invagination of the posterior part of the venter of the eighth abdominal segment posterior to the invagination that forms the median oviduct. Later, an inflection of the ventral body wall in this region encloses both the gonopore and the spermatic aperture, and itself becomes the vagina.

The spermatic apparatus of a female insect serves the purposes of receiving, storing, and discharging the sperm. In the flea it includes the bursa copulatrix with its duct opening from the vagina, and either two spermathecae with individual ducts from the bursa, or a single spermatheca with its own duct, and a blind duct. Presumably the presence of two spermathecae represents the more generalized condition, but most fleas have only one spermatheca. Paired spermathecae are said by Wagner (1939) to be present in the genera *Hystrichopsylla, Typhloceras, Coptopsylla,* and *Macropsylla*; in *Macropsylla hercules* Roths. one spermatheca is shown by Jordan (1921) to be smaller than the other.

In *Hystrichopsylla gigas dippiei* Roths. (pl. 15 I) the bursal duct is a relatively long, strong-walled tube (*Db*), arising apparently from a small aperture (*Ob*) in a shallow pocket of the vaginal wall, and leading into a flattened oval sack, the bursa (*Bcpx*), which has thick cellular walls. From the opposite (anterior) side of the bursa emerge the two spermathecal ducts (*Ds*) present in this species. The small lumen of the bursa appears to make an S-shaped bend, the entrance tube opening posteriorly into the upper arm, the spermathecal ducts arising from the other. Each spermathecal duct is ensheathed in a mass of large, soft gland cells, which increases in thickness toward the spermatheca. The right duct in the specimen illustrated is somewhat longer than the left duct.

Each spermatheca of *Hystrichopsylla gigas dippiei* (pl. 15 I, *Spt*) is a large, rigid, oval sack with a narrowed neck at the anterior end bent at a right angle to the axis of the organ. The distal part of the neck and the upper part of the sack have a ringed appearance due to fine circular ridges on the cuticular inner walls. The lower end of the sack is thickened and appears as a basal plate pierced by the duct. Stretched between the neck and the sack is a large bundle of muscle fibers (*mcl*). It has been said that the spermatozoa are stored in the neck of the spermatheca, but in *Hystrichopsylla gigas dippiei* the entire organ is filled with them (*Spz*).

Though the majority of fleas have only one spermatheca, apparently on the right side in all cases, the left duct usually persists with its sheath of gland cells (pl. 15 H, *Dob*). This blind duct has been termed by Dampf (1912) the "ductus obturatorius." However, since the duct is not an obstructing agent, but is itself occluded, it is more properly a *ductus obturatus*. The two ducts are generally united proximally in a common duct from the bursa (H, *Dsc*), which is of variable length, and sometimes coiled. The ductus obturatus, however, has a tendency to reduction and a loss of its gland cells. Its relative development in different species of fleas has been described by Dampf (1912), who shows that it may be shortened to a small blind appendage of the bursa, as in bird-inhabiting species of *Ceratophyllus,* and is finally lost in some species of this genus. The spermatheca itself varies in shape in different fleas, and its form often furnishes a good taxonomic character. The muscles attached on the spermathecal neck would appear by their contraction to bend the neck closer to the sack, and it is generally supposed that they thereby effect an expulsion of the sperm, though how the action can produce this result is not clear.

The bursa copulatrix is not in all fleas of so simple a structure as that of *Hystrichopsylla,* and there may be special features at the orifice of the bursal duct. In *Ctenocephalides felis* (Bouché) and *Pulex irritans* L. the site of the bursal entrance is marked by a depression in the anterior vaginal wall (pl. 15 C, D, E, F) margined below by a narrow transverse sclerite (D, E, F, G, *bb*). At the center of this depression is a small protruding lobe, which hangs like a valve over the bursal aperture (*Ob*). The bursal duct in *Ctenocephalides* is a short, wide passage (H, *Db*), which expands transversely into the lumen of the bursa. The bursa itself has the form of a hemisphere with double walls (G, H, *Bcpx*), being comparable to a hollow rubber ball with one side pushed in. The narrow lumen thus appears in optical section as a clear crescent between a thick convex upper wall of large cells and a thin concave lower wall (H). The short, wide entrance duct opens posteriorly into the bursal lumen (G), and the common spermathecal duct emerges from the concave under side of the organ (G, H). Seen in optical or actual longitudinal section (G), therefore, a bursa and its duct of this type appear to be an S-shaped tube, and have often been represented as such. Lass (1905) gives a correct account of the organ in *Ctenocephalides canis,* though his description is somewhat hard to follow.

Judging from published illustrations there would appear to be much variation in the length of the bursal duct in different fleas. Jordan and Rothschild (1915-1924) give figures of various species in which the duct is long and slender as in *Hystrichopsylla,* and a number of examples of a short, wide duct are illustrated by Sharif (1930). Most drawings of the bursa, however, appear to have been made from mounted specimens of whole fleas, and probably do not show the full form or structure of the organ.

A complex system of muscle fibers is associated with the bursa copulatrix and its duct, but no detailed study has been made of these bursal muscles, and no explanation can be given of the expulsory mechanism of the spermatic apparatus.

Accessory genital glands have not been generally observed in female fleas, and the writer has not with certainty seen any such glands. Lass (1905), however, described in *Ctenocephalides canis* a multicellular body with a central canal that opens above (posterior to) the bursal aperture, which he believes is a gland that may secrete an adhesive coating for the eggs.

VIII. THE MALE GENITALIA

The external genital organs of the male flea include a pair of two-segmented *claspers* intimately associated with the tergum of the ninth abdominal segment, and a large *intromittent organ* lying ventrally in the abdomen, with its distal part, the aedeagus, projecting externally above the ninth sternum. The structure of the claspers is well known to flea specialists, and the many modifications of these organs are amply illustrated in the literature of flea taxonomy. The intromittent organ, on the other hand, which is probably the most complex genital apparatus to be found in all the insects, has been but little studied, and since Wagner's early paper (1889) on *Vermipsylla alacurt* Schimk. until every recently no serious attempt has been made to understand its structure or to explain its mechanism. (See Sharif, 1945.)

The usual and typical structure of the external genital parts of the flea, and the relationship of the organs to the ninth and tenth abdominal segments in the adult insect are shown diagrammatically in figure 5. The clasper consists of a broad *clasper lobe* (*CL*) continuous with the lower end of the narrow ninth tergum (*IXT*), and of a movable distal appendage, commonly termed the *finger* (*F*). From the base of the clasper lobe a large apodemal arm, known as the *manubrium* (*Mnb*), extends forward into the abdominal cavity, and generally is continuous at its base with the lower end of the anterior apodeme of the ninth tergum (*tAp*). The continuity of the manubrium with both the clasper and the tergal apodeme would appear at first sight to constitute an anomalous condition, since the manubrium is invaginated mesad of the ninth abdominal sternum (*IXS*), that is, between the ninth and tenth abdominal segments, while the apodeme is an inflection from the ninth tergum between the eighth and ninth abdominal segments. The relation becomes anatomically possible by reason of the overlapping of the ninth sternum against the lower ends of its tergum. The claspers are seldom flexible on the ninth tergum, and have no musculature of their own, but the finger is movably articulated on the clasper lobe and is well provided with muscles arising in the latter, on the ninth tergum, and on the manubrium. In

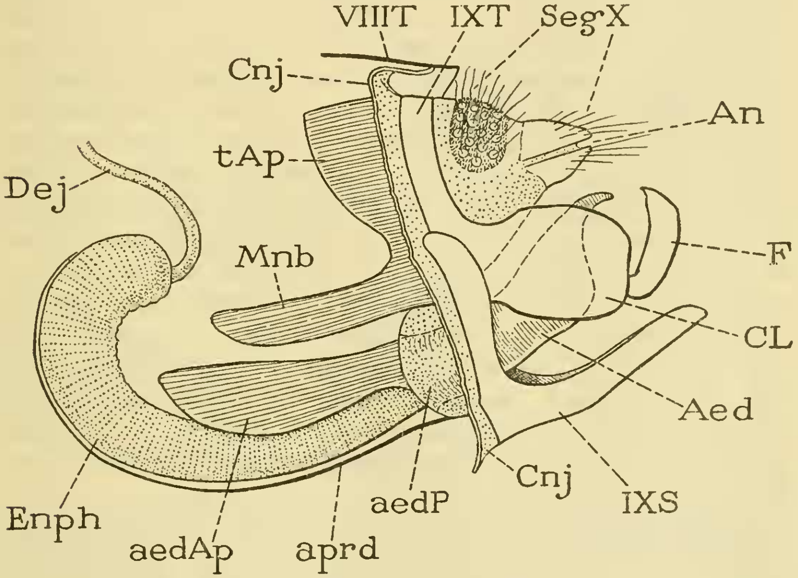

FIG. 5.—Diagram of the external male genital apparatus and its relations to the ninth and tenth abdominal segments, left side.

Aed, aedeagus; *aedAp*, aedeagal apodeme; *aedP*, aedeagal pocket; *An*, anus; *aprd*, apodemal rod of endophallic sack; *CL*, clasper lobe; *Cnj*, conjunctival membrane between segments *VIII* and *IX*; *Dej*, ductus ejaculatorius; *Enph*, endophallic sack; *F*, finger of clasper; *IXS*, ninth abdominal sternum; *IXT*, ninth abdominal tergum; *Mnb*, manubrium; *SegX*, tenth segment of abdomen; *tAp*, apodeme of tergum *IX*; *VIIIT*, eighth abdominal tergum.

some fleas an accessory movable process is closely associated with the movable finger.

The intromittent organ consists of the external *aedeagus* (fig. 5, *Aed*), which arises from a pocket (*aedP*) below the claspers embraced by the ascending arms of the ninth sternum (*IXS*), and of a large sacklike *endophallus* (*Enph*) invaginated from the aedeagus that extends forward into the base of the abdomen, where it turns upward and may be more or less coiled. The anterior end of the endophallus receives the ductus ejaculatorius (*Dej*). The aedeagal pocket (*aedP*) represents the inner end of the male genital chamber; its dorsal wall is continuous with the under surface of segment *X*, its ventral wall is reflected into the dorsal surface of sternum *IX*. From the base of the aedeagus arises a broad *aedeagal apodeme* (*aedAp*) that extends forward in the abdomen above the horizontal part of the endophallus. Below the endophallus and closely associated with it is a long, tapering *apodemal rod* (*aprd*), which arises in some fleas from the wall of the aedeagal pocket below the aedeagus, in others from the base of the ninth sternum, or again from the aedeagus itself. This rod is often called the "sternal apodeme," regardless of its variable connections; functionally it pertains to the endophallus. The fibers of an elaborate musculature attach on the manubrium, the aedeagal apodeme, the endophallic sack, the apodemal rod, and the ninth sternum. Both the aedeagus and the endophallus have a complex inner structure, which will be fully described later.

A comparison of the external genital structures of the male flea with those of other insects would suggest that the two-segmented claspers of the Siphonaptera are homologues of the similar organs (parameres) in Mecoptera, Trichoptera, and nematocerous Diptera. The only feature peculiar to the fleas is the union of the claspers with the tergum of the genital segment. The intromittent organ of the fleas, on the other hand, has the same relation to associated parts as in other insects, and even its complexities have counterparts elsewhere.

The early development of the flea genitalia has been observed in *Nosopsyllus fasciatus* (Bosc) by Sharif (1937), who says that the first genital rudiments appear in an early third-stage larva as a single pair of simple phallic lobes sunken into a pocket of the ventral conjunctiva between the ninth and tenth abdominal segments (fig. 6 C, *PhL*). At a late prepupal stage the lobes are everted from the pocket, and each lobe now splits into a lateral branch and a mesal branch (D, E, *Pmr, Mmr*). Later, the mesal branches (*mesomeres*) unite to form the aedeagus; the outer branches, Sharif says, "are the rudiments of the parameres." Unfortunately Sharif does not carry the development of the genital organs through to the pupal or adult stages, and it is not clear what organs of the adult he would here identify as "parameres"; in earlier taxonomic papers he follows the usual custom of giving this term to certain apical lobes of the aedeagus.

The genital structures present on the skin of a mature male pupa of *Ceratophyllus swansoni* Liu (fig. 6 A) consist of a median aedeagus (*Aed*), and of a pair of broad lateral lobes (*Pmr*) projecting from the ninth segment at the sides of the aedeagus. These lateral lobes of the mature pupa of *Ceratophyllus* certainly can be nothing other than the phallic *parameres* of earlier stages. They become the genital claspers of the adult, since the clasper lobe and finger of the imago are differentiated within the pupal organ. We may, therefore, confidently assert that the genital claspers of the Siphonaptera are parameral phallic derivatives homologous with the two-segmented claspers of Mecoptera, Trichoptera, and Diptera, and with the phallic parameres of Coleoptera and Hymenoptera. The

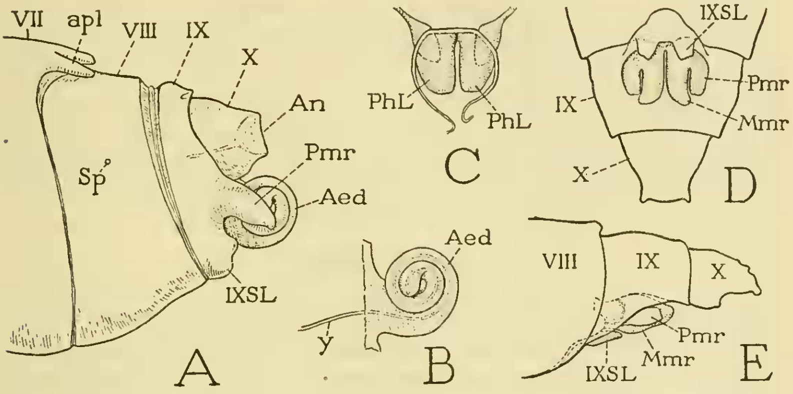

FIG. 6.—Development of the male external genitalia. (C, D, E from Sharif, 1937.)

A, mature pupal skin from end of abdomen of *Ceratophyllus swansoni* Liu, showing parameres, coiled aedeagus, and rudiments of ninth-sternal lobes. B, pupal aedeagus of same, showing aedeagal tube of imago inside the pupal organ. C, primary phallic lobes in "peripodal" pocket of third-stage larva of *Nosopsyllus fasciatus* (Bosc), together with ends of associated ducts. D, terminal abdominal segments of early male prepupa of same, ventral view, showing phallic lobes everted and each lobe cleft into an inner branch, or mesomere, and an outer branch, or paramere; also seen are the rudiments of the ninth-sternal lobes. E, lateral view of terminal abdominal segments of a late male pupa of same.

Aed, pupal aedeagus; *An,* anus; *apl,* antepygidial lobes; *IXSL,* lobe of ninth sternum; *Mmr,* mesomere; *PhL,* primary phallic lobe; *Pmr,* paramere; *Sp,* spiracle; *y,* tube of imaginal aedeagus in aedeagus of pupa.

basal lobe and the finger of the flea's clasper are, respectively, the "coxite" and the "stylus" of the "gonopod" in the usual terminology of the male genital organs, or the *basimere* and the *distimere* of the paramere according to the better nomenclature recently proposed by Crampton (1942, p. 86). That the parameres are "gonopods" is an unproved assumption, but, in any case, the names "exopodite" and "endopodite," sometimes used for the clasper lobe and the finger in descriptions of fleas, have no proper place in entomological terminology.

The aedeagus of the fleas attains to no complexity of development in the pupa. The pupal organ of *Ceratophyllus swansoni* is a simple tube, but is so long that it is thrown into a coil (fig. 6 A, B, *Aed*); in *Nosopsyllus fasciatus,* Sharif says the pupal aedeagus is curved upward and resembles the beak of a parrot. The elaborate structure of the adult intromittent organ is a product of the imaginal development that takes place entirely within the pupal skin.

THE CLASPERS

In most taxonomic papers on fleas the claspers are shown only as they have been seen in whole specimens cleared and mounted. Their structure and anatomical relations, however, are better determined by dissection, as illustrated from *Hystrichopsylla gigas dippiei* Roths. on plate 16. At A the apical segments of the abdomen are undisturbed; segments *VIII* and *IX* are mostly covered by the large tergal and sternal plates of segment *VII,* and the left clasper lobe (*CL*) is seen projecting beyond the latter. On removal of the plates of segment *VII* (*B*), the tergum and sternum of segment *VIII* are revealed, and the clasper is more fully exposed. Now, dissecting off the plates of segment *VIII* uncovers the ninth segment and the entire clasper (C), and finally, a removal of sternum *IX* and segment *X* (D) shows plainly the intimate relation of the clasper lobe with the ninth tergum. The tergal apodeme (*tAp*) is relatively small in *Hystrichopsylla* and has but narrow connections with the manubria (*Mnb*), though the latter are broadly continuous with the outer walls of the clasper lobes. The membranous inner walls of the lobes diverge from the midline of the body below the tenth segment (G), and in each mesal wall is a long rodlike sclerite (E, F, G, *cc*) proceeding from a small median plate (E, G, *dd*) between the bases of the lobes. Ventral to this plate the abdominal wall is inflected into the upper wall of the aedeagal pocket.

The movable finger of the clasper of *H. gigas dippiei* appears externally as a thick process projecting upward from beneath the basal lobe (pl. 16 C, D, *F*), but in a mesal (F) or a dorsal view (G) the finger is seen to be a V-shaped structure with a broad, flat anterior arm implanted in the membranous mesal wall of the lobe, and hinged to the latter at its upper end by a strong ball-and-socket articulation (F, *gg*). The fibers of a large fan-shaped muscle arising in the clasper lobe converge upon the articular arm of the finger, and serve apparently to depress the free posterior arm.

In a comparative study of any organ it is always desirable to distinguish a generalized type of structure from a specialized type. With respect to the fleas we have no accepted criterion for judging the order of evolutionary development, but in the relation of the claspers to the tergum of the genital segment three types of structure may be recognized that appear to have a developmental sequence. In the first type the clasper lobes are not intimately united with the ninth tergum, and there may or may not be a union of the manubria with the tergal apodeme. In the second type the clasper lobes are sclerotically continuous with the tergum. The third type of structure involves first a reduction of the ninth tergum almost to the point of obliteration (fig. 4 B, *IXT*), accompanied by a great enlargement of the tergal antecosta (A, *IXAc*) to form a large, phragmalike tergal apodeme (B, *tAp*), and second, a union of the apodeme on each side with the manubrium (*Mnb*) and the basal lobe of the clasper (*CL*). This curious modification produces a unified composite structure which clearly is all for the benefit of the claspers. The intersegmental muscles between tergum *VIII* and tergum *IX* include a pair of large fiber bundles (*dmcl*) arising on the under surface of tergum *VIII*, and attached ventrally and anteriorly on the upper surface of the ninth-tergal apodeme (*tAp*). These muscles evidently, by lifting the apodeme, cause a depression of the claspers.

The first type of structure in the clasper-tergum relation is here illustrated in *Ctenocephalides felis* (Bouché), *Pulex irritans* L., and *Echidnophaga gallinacea* (Westw.). It is assumed to represent the primary condition, since, if the claspers of the imago are the phallic parameres displaced laterally from the aedeagus, the union of the claspers with the genital tergum must be secondary.

In *Ctenocephalides felis* the ninth abdominal tergum of the male is a narrow sclerite arched over the back at the base of the pygidium (pl. 17 A, *IXT*); ventrally it widens on each side into a lateral expansion to which the clasper lobe (*CL*) is *flexibly* attached. The two large, rounded apodemal plates of the tergum (*tAp*) have no connection with the manubria (*Mnb*). The clasper lobes (*CL*) are broad and oval; their mesal surfaces come together in the posterior abdominal wall (B), but there is no median plate here as in *Hystrichopsylla.* The small movable finger does not have the usual apical position on the supporting lobe, but is articulated proximally on the latter (B, C, D, *F*) and lies below and within the base of the lobe. The finger is movable by a muscle (C, *mcl*) arising on the lower part of tergum *IX*. The manubria are forked at their bases (B, *Mnb*), the outer branch of each supporting the lateral lobe of the clasper (*CL*), the other the mesal finger (*F*). Though the manubria appear to be arms of the claspers, they arise largely from sclerotizations in the dorsal wall of the aedeagal pouch beneath the claspers, as can clearly be seen by spreading the claspers and looking into the pouch from behind.

Wagner (1939) gives a somewhat different interpretation of the clasper of *Ctenocephalides,* inasmuch as he regards the main lobe as an outer movable finger ("expodite"), and the small lobe as an inner movable finger ("endopodite"), both supported on the lateral expansion of the tergum, which he regards as the body of the clasper, or "gonopod." A comparison with *Pulex irritans* (pl. 17 E), however, suggests an identity of the large clasper lobe of *Ctenocephalides* with the similarly shaped lobe of *Pulex,* and the articulation of the small lower lobe in *Ctenocephalides* with the upper lobe bears out this interpretation. *Pulex* does have two movable fingers, but they are both on the inner surface of the main lobe (F).

In *Pulex irritans,* as in *Ctenocephalides felis,* the clasper lobes have no firm connection with the ninth abdominal tergum (pl. 17 E). Their outer walls, however, are directly produced into the apodemal manubria, and the bases of the latter are widely continuous with the lower parts of the large tergal apodeme. The presence of opposite marginal thickenings in the manubrio-apodemal sclerotization suggests that the two parts (*Mnb, tAp*) have been united secondarily. As in *Ctenocephalides* the manubrial bases are exposed in the dorsal wall of the aedeagal pouch (*aedP*) between the arms of the ninth sternum. The broad clasper lobe of *Pulex* (F) has rounded dorsal and distal margins, which are rolled mesally, forming a thick, setigerous, peripheral fold on the otherwise concave inner surface of the lobe. In the concavity of the mesal wall of the lobe are lodged horizontally two large processes (*F, F′*), one ventral the other dorsal, the shapes of which are shown at G. The lower process is supported on a strong basal thickening of the corresponding manubrium (F, G, *Mnb*), and evidently represents the movable finger of *Ctenocephalides* (D, *F*). The dorsal process (*F′*) is articulated proximally on the upper part of the base of the clasper lobe (F), and is clearly an accessory finger. Large groups of muscle fibers converge from the tergal apodeme, the manubrium, and the clasper lobe, which appear to be attached on each of the finger processes, so that the latter may act as a pair of pincers.

The genital claspers of *Echidnophaga gallinacea* differ in shape from those of *Ctenocephalides* and *Pulex,* but the essential structure is the same as in these genera (pl. 17 H). The outer clasper lobe of *Echidnophaga* is slender and elongate (*CL*) and has no firm connection with the narrow ninth tergum (*IXT*). Both the clasper lobe and the manubrium, however, are confluent with the lower end of the large tergal apodeme (*tAp*). Two movable fingers are present in *Echidnophaga* as in *Pulex,* but they both arise ventrally from the base of the lobe (H, I, *F*, *F'*). Broad sheets of muscle fibers (I) arising on the tergal apodeme and within the clasper lobe converge to the bases of the fingers, but, if correctly observed, are all inserted on the larger lower finger (*F*) distal to the articulation of the latter on the manubrium.

In the second type of structure pertaining to the ninth tergum and the claspers, the sclerotic outer walls of the clasper lobes have an unbroken continuity with the tergum. This condition is most obvious in *Hystrichopsylla* (pl. 16 H) in which the ninth tergum is a relatively wide sclerite (*IXT*). It is seen also in *Thrassis acamantis* (Roths.), though in this species the tergum is reduced to a narrow band (pl. 17 K, *IXT*) supporting the large tergal apodeme (*tAp*), but which widens laterally where it merges into the clasper lobes (*CL*). The movable finger of these species arises distally on the clasper lobe; that of *Hystrichopsylla gigas dippici* has already been described (pl. 16 F), the finger of *Thrassis acamantis* (pl. 18 C, *F*) is of similar shape but less strongly bent, and is doubly musculated.

The third type of structure in the tergal relations of the claspers is but an exaggeration of the second, since it is brought about by an extreme reduction of the external part of the genital tergum, with the result that the clasper lobes and manubria appear to be lateral expansions of the tergal apodeme. This type of structure is characteristic of the majority of the fleas, but it clearly represents a specialized condition, and is one peculiar to the Siphonaptera. It is discussed at some length by Wagner (1932), and is illustrated by him from *Ceratophyllus penicilliger* (Grube). Examples of it are here shown in *Trichopsylla vison* (Baker) (pl. 17 J), *Dactylopsylla bluei* (C. Fox) (pl. 17 L), *Trichopsylla eumolpi* (Roths.) (pl. 17 M), and *Opisodasys pseudarctomys* (Baker) (pl. 18 B). In these and other genera of like structure, the ninth tergum, as already noted, is represented only by the line at the base of the apodeme on which are attached the intersegmental conjunctival membrane from the eighth tergum before it, and that to the tenth segment behind it. The tergal apodeme, on the other hand, is highly developed and is broadly continuous on each side with both the manubrium and the clasper lobe. The separation of the apodemal parts of this composite structure from the external lobe of the clasper is marked on each side by the attachment line of the conjunctival membrane from the eighth segment (pl. 18 B, *Cnj*), but this line is seldom to be seen in specimens cleared and mounted as they are usually studied.

An intermediate condition in which the ninth tergum is still a recognizable sclerite is shown by Wagner (1932) to be present in *Neopsylla*, and a similar condition is seen in *Arctopsylla ursi* (Roths.) (pl. 21 A), in which the narrow ninth tergum (*IXT*), tapering upward from the clasper, represents a stage of reduction differing only in degree from that in *Thrassis acamantis* (pl. 17 K).

In species of this third type of structure the movable finger of the clasper is generally articulated on the distal margin of the basal lobe and projects freely beyond the latter (pl. 17 J, L, M; pl. 18 A, B; pl. 21 A). An accessory immovable process of the lobe (*ff*) is commonly present, and in some cases two such processes (pl. 18 B). The clasper lobe itself usually projects well beyond the supporting apodeme, but it may be so reduced in size as to appear merely as a lateral area of the segment between the tergal apodeme and the manubrium (pl. 17 L, *CL*).

THE INTROMITTENT ORGAN

The complex apparatus by which the male flea accomplishes the insemination of the female consists, as already noted, of an external part, the *aedeagus* (fig. 7, *Aed*), bearing a large basal apodeme (*aedAp*), and of an internal part, or *endophallus* (*Enph*), invaginated from the aedeagus. Each of these parts is in itself a complex structure.

The aedeagus.—In the flea, as in other insects, the aedeagus arises from a membranous pouch between the base of the tenth abdominal segment and the base of the ninth sternum (fig. 5, *aedP*). The basal wall of the pouch (fig. 7, *ee*) marks the line between the aedeagus proper (*Aed*) and its apodeme (*aedAp*), but in cleared specimens the pouch is not visible, and the aedeagus and its apodeme appear as one continuous structure, as in fact they are. The external part of the aedeagus (fig. 7, *Aed*) is usually a fairly simple, cylindrical body projecting posteriorly and upward above the ninth abdominal sternum. The distal part of the organ is deeply invaginated to form a large *end-chamber* (*EC*), which is widely open posteriorly and more or less ventrally. The margins of the opening are usually produced into apical lobes; typically there is a median *dorsal lobe* of variable shape (pl. 18 D; pl. 19 N; pl. 20 G, *mm*), and a pair of broad *lateral lobes* (*nn*), which are mere expansions of the side walls of the end-chamber. Some of the apical lobes of the aedeagus are commonly called "parameres" by flea taxonomists, but, as already shown, the true phallic parameres of the flea become the claspers. The end-chamber of the aedeagus contains an aedeagal *inner tube* (fig. 7, *ITu*) arising from the inner wall of the cavity, and usually a pair of movable hooks, or *crochets* (*Crc*), arising from the lateral walls. The aedeagal apodeme (*aedAp*) is an extension from the dorsal and lateral walls of the base of the aedeagus into the body cavity. Superficially the apodeme appears as a flat plate, but in transverse section it is seen to consist of three lamellae (B), the lateral plates (*LP*) forming together an inverted U, from which apparently the middle

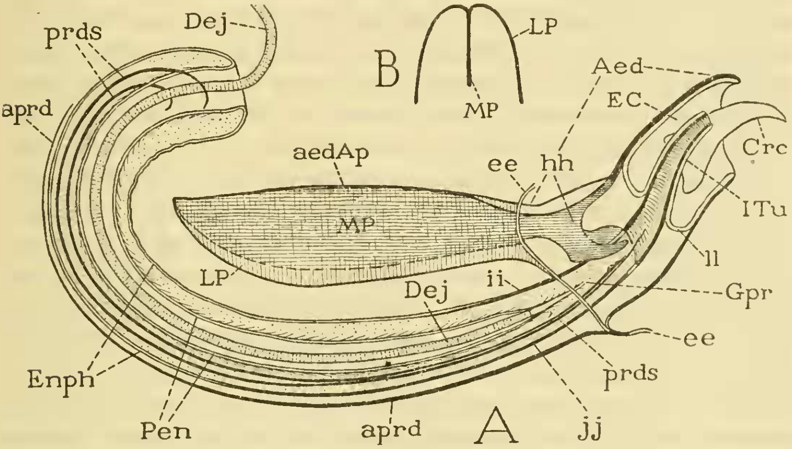

FIG. 7.—Diagram of the male intromittent organ, with the terminology here used for its parts.

A, lateral view of the entire organ; the line *ee* represents the base of the aedeagal pouch, which separates the external aedeagus (*Aed*) from the internal aedeagal apodeme (*aedAp*) and the endophallus (*Enph*). B, cross section of aedeagal apodeme.

Aed, aedeagus; *aedAp*, aedeagal apodeme; *aprd*, apodemal rod of endophallus; *Crc*, crochet (of right side); *Dej*, ductus ejaculatorius; *EC*, end-chamber of aedeagus; *ee*, base of aedeagal pouch; *Enph*, endophallic sack; *Gpr*, gonopore; *hh*, fulcral strut of middle plate of apodeme supporting inner tube of aedeagus; *ii*, dorsal intramural rod of endophallus; *ITu*, inner tube of aedeagus; *jj*, ventral intramural rod of endophallus; *ll*, inner wall of aedeagal end chamber; *LP*, *MP*, lateral and middle plates of aedeagal apodeme; *Pen*, penis; *prds*, penis rods.

plate (*MP*) is a median inflection. The middle plate, however, is continued into the base of the aedeagus (A, *MP*) as an inflection from a deep median groove of the dorsal wall of the latter, and gives off here a strong strut (*hh*) that forms a supporting apparatus for the inner tube of the aedeagus.

The inner tube of the aedeagus (fig. 7 A, *ITu*) is an evagination of the inner wall (*ll*) of the aedeagal end-chamber, which at the tube apex is again invaginated to form the inside wall of the tube. The mouth of the tube, therefore, is the true external opening of the aedeagus; the channel of the tube leads directly into the lumen of the endophallus (*Enph*). The inner tube varies in shape and in length in different fleas; usually it is confined to the end-chamber of the aedeagus, but in some species it extends far out of the latter. The sclerotic inner wall of the tube is continued below the wall of the end-chamber, and usually forms here a thickened basal part of the tube, which is supported on the strut from the middle plate of the apodeme. The apodemal strut ends in an enlargement which divides into three lobes (pl. 20 M; pl. 21 G, *hh*), a broad median lobe (*oo*) presented against the dorsal edge of the basal foramen of the tube, and a pair of slender lateral lobes (*pp*) that articulate on the sides of the foramen and serve as fulcral points for movement of the tube. On the proximal part of the tube are inserted a pair of levator muscles (pl. 20 J, *73*) arising dorsally in the base of the aedeagus, and a pair of depressor muscles (*74*) arising ventrally and inserted by a common tendon. The tube is thus movable on the support in a vertical plane, but it is not protractile from the aedeagus.

The aedeagal crochets are typically flat, hook-shaped structures with their points directed posteriorly (fig. 7 A, *Crc*). They are highly variable in shape and size, however, being sometimes reduced to a pair of small plates, and in some cases they appear to be absent. Each crochet has a single long muscle attached by a tendon on its base (pl. 20 O, *72*), the fibers of which arise proximally in the aedeagus and along the entire length of the inner face of the corresponding lateral plate of the aedeagal apodeme.

The endophallus.—The endophallus of a male insect is either the original space enclosed by the union of the median phallic lobes that form the aedeagus, or it is a secondary invagination from the mouth of the aedeagus. It may be a simple pouch, or vesica, usually eversible, or it may be a long eversible tube, which, when everted, carries the gonopore on its extremity. Again, however, the primary endophallic tube may contain a secondary tube evaginated from its inner end, which carries the gonopore, and, by eversion, serves as a penis. The aedeagus itself is seldom the entering part of the intromittent apparatus.

The endophallus of the flea is a highly complex structure. Its outer wall forms a long, cylindrical, thin-walled sack (fig. 7, *Enph*) continuous from the inner wall of the inner tube of the aedeagus, which extends forward beneath the aedeagal apodeme and curves upward around the anterior end of the latter, where it may be more or less coiled upon itself. The walls of the sack are strengthened by a dorsal and a ventral linear thickening of the intima (*ii, jj*). To distinguish these rodlike structures from other true rods of the endophallus they are here termed the *intramural rods.* The dorsal intramural rod (*ii*) is usually short and may be absent, but the ventral rod (*jj*) can generally be traced through at least the proximal half of the endophallic wall. The entire length of the sack is ensheathed in circular or semicircular muscle fibers, which in the region of the intramural rods are attached on the latter. Beneath the endophallus, but closely following its ventral curvature, is a free *apodemal rod* (*aprd*). This rod arises at the base of the aedeagus, in some fleas from the wall of the aedeagal pouch, in others from the ninth sternum, and in still others from the aedeagus itself. It is usually much longer and more conspicuous than the intramural rods, and may extend almost to the extremity of the endophallic sack. It gives attachment to an outer sheath of endophallic muscle fibers arising dorsally on the aedeagal apodeme.

At the inner extremity of the endophallus the wall of the sack is invaginated into the lumen to form a more slender inner endophallic tube (fig. 7 A, *Pen*) that goes back again to the base of the aedeagus, where it ends with a narrowed, tapering, apical section. This inner tube of the endophallus, finally, is traversed throughout its length by the ejaculatory duct (*Dej*), which discharges through a fine exit canal opening by a minute aperture on the end of the tube (*Gpr*). Since this aperture is the true gonopore of the male flea, the tube containing the exit genital duct may be termed the *penis* (*Pen*), though in the flea it does not itself convey the sperm into the receptaculum of the female. The penis, in fact, is too thick even to be exserted through the canal of the inner tube of the aedeagus. Its outer wall is usually clothed with slender, closely appressed setae directed posteriorly (which have been mistaken for spermatozoa).

The penis is always accompanied by a pair of long, slender *penis rods* (fig. 7 A, *prds*). The rods arise in the anterior end of the endophallic sack against the sides of the penis, one right, the other left, and follow the convex side of the latter back to the base of the aedeagus. Below the horizontal part of the penis the rods converge and become adherent, though they slide freely on each other. (The nature of the union has not been determined by sections of the rods.) On the bases of the rods are attached muscles from the wall of the endophallic sack; the distal ends extend somewhat beyond the tip of the penis, and are usually more or less differentiated in form (pl. 18 F, K; pl. 19 L; pl. 20 D, K, S; pl. 21 I). It is not unlikely that the end shapes of the rods may be found to be characteristic of genera or species. The penis rods are the only elements of the intromittent apparatus that are capable of being protracted from the aedeagus, and they alone enter the bursal aperture of the female.

In an elaborate study of the male genital organ of the oriental cat flea, received too late for a full discussion, Sharif (1945) makes some very different interpretations from those given above. The external part of the organ is regarded as an extension from the ninth and tenth abdominal sterna; the internal sack is therefore interpreted as a "phallothecal chamber," and the inner tube as the true aedeagus. A sperm "pumping apparatus" is described in detail, but no such structure has been observed, or, at least, so interpreted, by the writer.

SPECIFIC EXAMPLES OF THE INTROMITTENT ORGAN

The following descriptions of the intromittent apparatus in 10 species of fleas, representing 9 genera, probably will show the principal types of structural modifications of the organ that occur in the flea order, but only a more entensive study will determine what value the genital characters may have for taxonomic purposes.

Ctenocephalides felis (Bouché) (pl. 18 D-G).—The aedeagus (D, *Aed*) is strongly up-curved distally, flaring at the extremity, and swollen at the base. The distal end is produced into a slender, median dorsal lobe (*mm*) and a pair of broad, thin lateral lobes (*nn*), between which is the end-chamber that contains the inner tube and the crochets (E). The aedeagal apodeme (D, *aedAp*) consists of three plates, but the large lateral plates are thin and transparent except for a thickened midrib (*kk*) running lengthwise through each plate. The narrow, distally expanded middle plate (E, *MP*), by contrast, is strongly sclerotized, and a superficial examination of a specimen, therefore, is likely to give the impression that there are three separate apodemal processes arising from the base of the aedeagus, if the outlines of the transparent lateral plates are not observed (E). In the base of the aedeagus the middle plate of the apodeme gives off a strong strut (E, *hh*) for the support of the inner tube of the aedeagus. The part of the tube that projects into the end-chamber is short (E, *ITu*), and bears a long process (*qq*) curving upward close against the anterior wall of the chamber, to which it is closely adherent, though it separates completely under pressure. The thick basal part of the inner tube that lies below the wall of the end-chamber (*ll*) articulates by lateral processes with the supporting strut from the middle plate of the apodeme, and from its proximal foramen is continued the membranous wall of the endophallic sack (*Enph*). A prominent, semicircular lobe (*rr*) on the base of the tube supports the ventral intramural rod (*jj*) of the endophallus. The apodemal rod of the latter (*aprd*) arises from the membranous wall of the aedeagal pocket below the base of the aedeagus.

The aedeagal crochets of *Ctenocephalides felis* are very small. They have the form of flat hooks with short recurved tips, which in side view may usually be seen projecting slightly from between the posterior margins of the lateral apical lobes of the aedeagus (D, E, *Crc*).

The endophallic sack curves upward around the anterior end of the aedeagal apodeme (D, *Enph*), but it is not coiled. The penis is a simple, thick, tapering tube (D, F, *Pen*), accompanied by the penis rods (*prds*), which are unusually large. The ends of the rods are markedly differentiated in shape (F); in the natural position the thickened end of the left rod securely clasps the slender right rod (G).

Echidnophaga gallinacea (Westw.) (pl. 18 H-K).—Externally the short aedeagus is simple, somewhat tapering, and blunt (H, *Aed*); the apodeme (*aedAp*) is relatively large. The end of the aedeagus, however, presents a small, deeply emarginate dorsal lobe (J, *mm*), a pair of broad, pointed lateral lobes (I, *nn*), and in addition, a pair of small ventral lobes. Lying mesad of the lateral lobes are the hook-shaped crochets (*Crc*), their sharp points directed toward each other giving them the appearance of a pair of nippers. Each crochet has a long, thick tendon (*t*) on which its muscle is attached. The inner tube of the aedeagus (H, *ITu*) is a simple, slender structure with a thickened base. The endophallic sack (H, *Enph*) and the organs within it (K) differ but little from these parts in *Ctenocephalides,* except that the penis rods (K, *prds*) are much slenderer and but little differentiated at their extremities. The apodemal rod of the endophallus (H, *aprd*) arises from the base of the aedeagus.

Hystrichopsylla gigas dippici Roths. (pl. 19 A-L).—The aedeagus of this species is a large, thick, conical structure (A, B, *Aed*), simply truncate at the end, without apical lobes. The dorsal surface of the organ proximally is channeled by a deep median depression (D), the dense lower walls of which are conspicuous by their dark color when seen from the side with transmitted light (E). The trough of this channel runs out on the middorsal line of the small aedeagal apodeme (*aedAp*), and is continuous with the middle plate of the apodeme, which latter in cross section (C) shows the usual triple structure.

The crochets and the inner tube of the aedeagus lie entirely within the end-chamber of the latter (E, *Crc, ITu*), which is open distally and ventrally. The crochets are reduced to a pair of small, sharply ridged plates implanted side by side in the dorsal wall of the aedeagal cavity (F, *Crc*) with their tips slightly projecting on the apical margin. Just proximal to the crochets is a second pair of much smaller sclerites giving attachment to strong tendons on which are inserted muscles corresponding to the crochet muscles of other species.

The inner tube of the aedeagus is exceptionally small in *Hystrichopsylla*. It has the form of a short spout (F, G, J, *ITu*) projecting from a large basal plate (*ss*) in the dorsal and inner wall of the aedeagal end-chamber, with a pair of thick arms diverging proximally to the supporting apparatus (E, G, *hh*). The support is a short strut given off directly from the inner face of the inflected dorsal wall of the aedeagus, which is continued into the middle plate of the apodeme. Its large, rounded median lobe (I, *oo*) fits into the dorsal emargination of the basal plate of the inner tube (J), and its small lateral processes (I, *pp*) articulate with the basal arms of the tube plate. The relation of the tube and its plate to the support is best seen in side view as shown at G. The inner tube of the aedeagus in *Hystrichopsylla* would appear to be capable of little movement; if muscles are connected with it they were not observed. The sclerotic walls of the funnel-like basal entrance to the tube (J), and the concave under surface of the median lobe of the support (I) are directly continued into the membranous walls of the endophallic sack. The ventral intramural rod of the latter appears as a thickening in the lower wall (J, *jj*) immediately before the base of the tube.

The endophallic sack of *Hystrichopsylla* curves upward around the anterior end of the aedeagal apodeme (pl. 19 A, B, *Enph*) and here receives the ductus ejaculatorius (*Dej*). The penis and the penis rods (K) have no distinctive features except in their terminal parts. The penis ends with a long, tapering, slightly up-curved apical section (L, *Pen*), the outer wall of which is extremely delicate and covered with fine setae, while the strongly sclerotic inner wall, supported on four prongs in the membranous part of the penis before it, forms an exit canal for the ductus ejaculatorius (*Dej*) running out to a needlelike point. At H the end of the penis is shown in the same enlargement as the inner tube of the aedeagus at J, from which it is evident that only the tapering apical section of the penis might be thrust through the narrow channel of the tube. The two penis rods are normally adherent along their distal parts; the slenderer rod ends with a truncate tip (L), the other with a spearheadlike enlargement. The apodemal rod of the endophallus arises far within the base of the aedeagus (E, D, *aprd*).

Pulex irritans L. (pl. 19 M-Q; pl. 20 A-E).—The position of the retracted intromittent organ in the abdomen is seen at M of plate 19. The aedeagus (*Aed*) is entirely enclosed by the large sternal plates of the eighth segment; the long endophallus (*Enph*) reaches into the second segment, and is here coiled upward to the right of the aedeagal apodeme between the broad manubria of the claspers. The entire organ removed, together with a part of the aedeagal pouch, is shown more enlarged at N.

The aedeagus of *Pulex irritans* (pl. 19 N, *Aed*) is cylindrical, enlarged at the end, and provided with well-developed apical lobes. The dorsal lobe (*mm*) forms a large, deeply emarginate, hoodlike covering over the single median crochet (*Crc*); the lateral lobes are simple quadrate expansions of the side walls of the end-chamber of the aedeagus. The slender aedeagal apodeme (*aedAp*), which is composed of the usual three plates (P), enlarges distally and bears on its upper surface a high, finlike crest. The inner tube of the aedeagus (N, *ITu*) is long, slender, and tapering; its thick base is supported in the usual manner on a strut (*hh*) from the middle plate of the apodeme. *P. irritans* has but a single aedeagal crochet (*Crc*), which is a flat median hook arising from the dorsal wall of the aedeagal end-chamber immediately beneath the hoodlike dorsal lobe (*mm*). The hook is set into a bilobed pad of the aedeagal wall (Q), and from lateral expansions of its base in the concave wall of the pad arises a flat, bifurcate tendon giving attachment to a pair of large muscles (*72*). This single, doubly musculated hook of the aedeagus of *P. irritans,* therefore, evidently represents the paired crochets of other species. The aedeagus, drawn as it appears in cleared specimens examined with transmitted light, is shown at O of plate 19. Certain details of internal structure are here seen more clearly than in ordinary dissections, but their anatomical relations would not be easily understood.

The coiling of the inner end of the endophallus, as seen in *Pulex,* is characteristic of many fleas, and in some species the coiling may be even more extensive. The spiral winding of the sack involves a corresponding coiling of the penis, the penis rods, the intramural rods, and the apodemal rod, presenting all together, as seen in transparent mounts of the whole insect, a confusing picture of many things encircling one another (pl. 20 A), often likened to a watch spring. When the various rods of the coil are separated, however, the spiral of each rod (B) is seen to be very simple; the endophallic sack of *Pulex,* in fact, makes only a loop and a half upon itself (pl. 19 N).

The penis and the penis rods of *P. irritans* are shown at C of plate 20, the ends of the rods more enlarged at D, and the reverse side of the larger rod at E. The ventral intramural rod (pl. 19 N, O, *jj*) arises from a prominent basal lobe (*rr*) of the inner tube of the aedeagus. The apodemal rod takes its origin from a small plate in the ventral wall of the aedeagal pouch (N, O, *aprd*).

Dactylopsylla bluei (C. Fox) (pl. 20 F-P).—This large species was found to be an excellent subject for dissection of the intromittent organ, and for a study of the structural details and internal musculature of the aedeagus. The ninth and tenth abdominal segments and the entire genital apparatus with its parts undisturbed are shown at F of plate 20. The large aedeagus (*Aed*), arising from its pouch (*aedP*) between the ascending arms of the ninth sternum (*IXS*), turns upward above the posterior arms of the sternum; the endophallus (*Enph*) extends forward from the aedeagus, curves dorsally around the end of the aedeagal apodeme, and is reflexed ventrally but not coiled. The intromittent organ separated from its surroundings is shown at G. The aedeagus (*Aed*) bears distally a slender, decurved dorsal lobe (*mm*), and a pair of large, oval lateral lobes (*nn*) with notched upper margins. Projecting from between the lateral lobes are seen the ends of the crochets (*Crc*), and between the latter the extremity of the inner tube beneath the protecting dorsal lobe. The relatively small aedeagal apodeme (*aedAp*) turns upward at its tapering anterior end; in cross section (H) it is seen to be trilamellate. The middle plate of the apodeme (I, *MP*) extends into the base of the aedeagus and gives off a long strut that forms the support (*hh*) of the inner tube of the aedeagus (*ITu*).

Beyond the base of the inner tube, the end-chamber of the aedeagus is widely open between the lower margins of the lateral lobes, but the membranous ventral wall of the proximal part of the aedeagus is continued into a median lobe of the chamber that partially ensheaths the inner tube (I, L, *tt*). The truncate end of this inner-tube sheath has an armature on its anterior side (N) consisting of a pair of small, triangular lateral plates with free apical points, and an elongate median sclerite descending from between the lateral plates, which itself bears two sharp processes, and tapers downward into the wall of the end-chamber that is reflected upward into that of the long dorsal lobe (I). Closely appressed against the sides of the sheath lobe (L, *tt*) are the large, flat crochets (*Crc*).

The inner tube of the aedeagus of *D. bluei* is long, slender, and slightly sinuous (I, J, *ITu*) ; ordinarily it stands vertically in the aedeagal end-chamber (I), projecting distally from its sheath (*tt*), with the apex beneath the decurved dorsal lobe of the aedeagus (*mm*). The strong inner wall of the tube forms a basal thickening of the latter (J), which gives off anteriorly a short process into the wall of the sheath (*tt*), and proximally articulates with the supporting strut (*hh*) from the middle plate of the apodeme (I). The support has the typical tripartite structure (M, *hh*), consisting of a weak median lobe (*oo*) that abuts against the base of the tube, and a pair of strong lateral articular processes (*pp*), on which the tube is movable in a vertical plane. On the base of the tube are attached the tendons of two levator muscles and two depressor muscles. The levators arise dorsally in the sides of the base of the aedeagus (I, *73*), and are inserted individually on the upper surface of the tube (J, *73*). The two depressors arise ventrally in the aedeagus (I, J, *74*), but both muscles are inserted by a common median tendon attached to a short ventral process of the base of the tube.

The crochets are large, flattened plates with long apical points directed posteriorly and freely exposed beyond the lateral apical lobes of the aedeagus (F, G, I, *Crc*). The broad basal parts of the crochets lie at the sides of the ensheathing lobe of the inner tube (L), and each bears laterally a small, recurved, spatulate process (L, P). Each crochet is movable on the lower angle of its base, and well above the latter is attached the tendon of its muscle, the fibers of which (O, *72*) arise along the entire length of the aedeagal apodeme and in the base of the aedeagus itself. The points of the crochets are lifted by the contraction of the muscles.

The endophallus of *D. bluei* needs no special description since it does not differ essentially from that of other species. Its apodemal rod (G, *aprd*) arises in the ventral wall of the aedeagal pocket (*aedP*). The penis ends with a sharply tapering point (K), the penis rods are slender and have but slight apical differentiations.

Thrassis acamantis (Roths.) (pl. 20 Q, R).—The principal external features of the intromittent organ to be noted in this species (Q) are the flat, laterally extended wings of the dorsal lobe of the aedeagus (*mm*), the small ventral hooks of the lateral lobes, and the great size of the crochets (*Crc*), the points of which project far beyond the aedeagus. The upper edge of each crochet is serrate (R), the outer surface bears proximally a small papilliform lobe. The crochet is strongly angulated, or sigmoid, in form and turns on the lower angle of its base. The tendon of its muscle (*72t*) is attached so far beyond and above the point of articulation as to give the muscle a powerful lifting effect on the distal hook. The reason for this reverse movement might be understood if the function of the crochet were known. The inner tube of the aedeagus (Q, *ITu*), its support (*hh*), and the middle plate of the apodeme (*MP*) have the usual structure and relations.

Arctopsylla ursi (Roths.) (pl. 21 A).—The figure of this species is drawn from a cleared and mounted specimen, and shows only the sclerotic parts of the genital apparatus ordinarily seen in such preparations. The unusually large aedeagus (*Aed*) is fully exposed at the end of the abdomen, where it stands almost vertically above the small ninth sternum, and at a right angle to its horizontal apodeme (*aedAp*). The bifid dorsal lobe of the aedeagus (*mm*) completely overhangs the end of the organ and conceals the slender, decurved terminal part of the long inner tube (*ITu*). The crochets (*Crc*) are deeply inserted within the end-chamber of the aedeagus.

Trichopsylla vison (Baker) (pl. 21 B-E).—The figure at B represents the distal half of the male abdomen drawn from a cleared and mounted specimen, showing the sclerotic parts of the genital apparatus in place, and their relation to the eighth and ninth abdominal sterna. When the intromittent organ is dissected out (C) it is seen to have a relatively simple form, with no angulation between the aedeagus and the apodeme. There is no preceptible dorsal lobe of the aedeagus, but the lateral lobes (*nn*) are large vertical plates. With transmitted light the inner parts of the aedeagus come into view (D), but they are better seen when isolated by dissection (E). The inner tube (*ITu*) has a thick conical base within the end-chamber of the aedeagus, but it is produced into a long vermiform distal part that extends out of the chamber and is ordinarily folded between the lateral lobes of the aedeagus (D). In the specimen drawn at B the tube is turned posteriorly and partly exposed at the end of the abdomen. Wagner (1939, fig. 98) shows in his figure of *Choriostopsylla ochi* Roths. a similar tube designated the "penis," and represented (certainly erroneously) as a direct continuation of the ejaculatory duct. The intra-aedeagal base of the tube is supported in the usual manner on a strut from the middle plate of the apodeme (D, *hh*).

The apparent crochets of *T. vison* are a pair of small plates lying just above the base of the aedeagal inner tube (D, E, *Crc*). These plates would hardly be recognized as the crochets were it not for the large muscles (*72*) from the aedeagal apodeme inserted by long tendons on their bases.

Trichopsylla eumolpi (Roths.) (pl. 21 F).—In this species the general structure of the intromittent apparatus is similar to that of *T. vison*, but the lateral lobes of the aedeagus (*nn*) are relatively larger, and the external part of the inner tube (*ITu*) is so long that, if stretched out, it would reach far beyond the end of the aedeagus. Normally the tube is bent upon itself and folded back between the large lateral aedeagal lobes.

Ceratophyllus swansoni Liu (pl. 21 G-I).—The intromittent apparatus of this species is remarkable for the extraordinary length of the inner tube of the aedeagus (I, *ITu*). The base of the organ is a thick, conical, darkly sclerotized body standing vertically on its support (*hh*) in the end-chamber of the aedeagus. From its apex is extended a long, slender, thin-walled, extra-aedeagal tube, which is abruptly turned downward and forward from the base, with the distal part bent upward. Usually this outer tube is entirely concealed in the space between the aedeagus and the ninth abdominal sternum, so well concealed, in fact, that perhaps few students of fleas have been aware of its existence; it is neither mentioned nor figured in the original description of the species (Liu, 1935). Probably the living flea keeps the tube in seclusion, but in an occasional dead specimen it may be seen fully extended from the end of the abdomen.

The conical base of the aedeagal tube presents a triangular dorsal surface (G, H, *ITu*), on the distal part of which are two prominent ridges that end in a pair of apical points projecting above the root of the slender outer part of the tube (I). The proximal angles of the base diverge widely in two socket-bearing arms (G, H) that articulate with the lateral processes of the support (G, *pp*). The broad median lobe of the supporting structure (*oo*) covers the entrance to the endophallic sack. If the support is removed from the base of the tube, the proximal foramen of the latter is exposed (H), and in the adhering lower wall of the endophallic sack is seen the ventral intramural rod (*jj*), above which are the free ends of the slender penis rods (*prds*) directed toward the channel of the tube.

COPULATION

It is hard to imagine why a male insect should need, for the mere transfer of sperm to the female, an organ so elaborate in structure and so complex in its mechanism as is the intromittent apparatus of the fleas; and it can only be inferred from the structure of the organ how the latter accomplishes its purpose. The aedeagus is to a small extent protractile from its pouch between the arms of the ninth abdominal sternum, and it may be partially inserted into the genital chamber of the female. The inner tube, being firmly articulated on its basal support within the aedeagus, is movable in a vertical plane by its own muscles, but is in no degree capable of protraction. The penis is a membranous, nonmuscular tube, of which only the tapering distal end, bearing the outlet of the ejaculatory duct, is of a size that would permit intrusion into the narrow canal of the inner tube of the aedeagus. The slender penis rods alone are capable of being thrust through the aedeagal tube of the male, and they only could enter the minute aperture of the female that gives access to the bursa copulatrix. These rods, therefore, must be the agents that carry the sperm from the gonopore of the penis and effect its transfer into the receptacle of the female.

During mating, as is well known, the male flea takes a position beneath the female, and apparently the genital claspers effect the union of his abdomen with the abdomen of the female. According to Lundblad (1927), however, the male first grasps the female beneath the base of the abdomen with his extended antennae, and by means of these organs secures a firm hold before attempting to unite the end of his abdomen with that of the female. The grip of the antennae is so effective that the struggling female is seldom able to free herself, and is thus held during the entire period of copulation. Lundblad's observations were made on *Ceratophyllus gallinae* Schrank, in which species, as in many others, the antennae of the male are much longer than those of the female, and are strongly erectile.

No published account known to the writer gives any specific information as to what takes place after copulation is effected. The minute opening of the bursa copulatrix in the wall of the vaginal passage is ordinarily covered by the overlying eighth sternum (pl. 15 B), and the latter must be depressed in order to expose the bursal orifice (D, *Ob*). The aedeagal crochets with their strong muscles must have some important function, but when the crochets are hook-shaped their points are turned in the wrong direction to grasp the edge of the female's eighth sternum, and moreover their muscles are so attached as to have a releasing action on the hooks, while finally, the crochets are variable in position and do not always have the form of hooks.

Through the interest of Dr. William L. Jellison, of the U. S. Public Health Laboratory at Hamilton, Mont., the writer has received for study a slide-mount of a male and female of *Ceratophyllus swansoni* Liu killed in copula. In this preparation, illustrated at B of figure 8, the female is erect on the end of the male's abdomen.

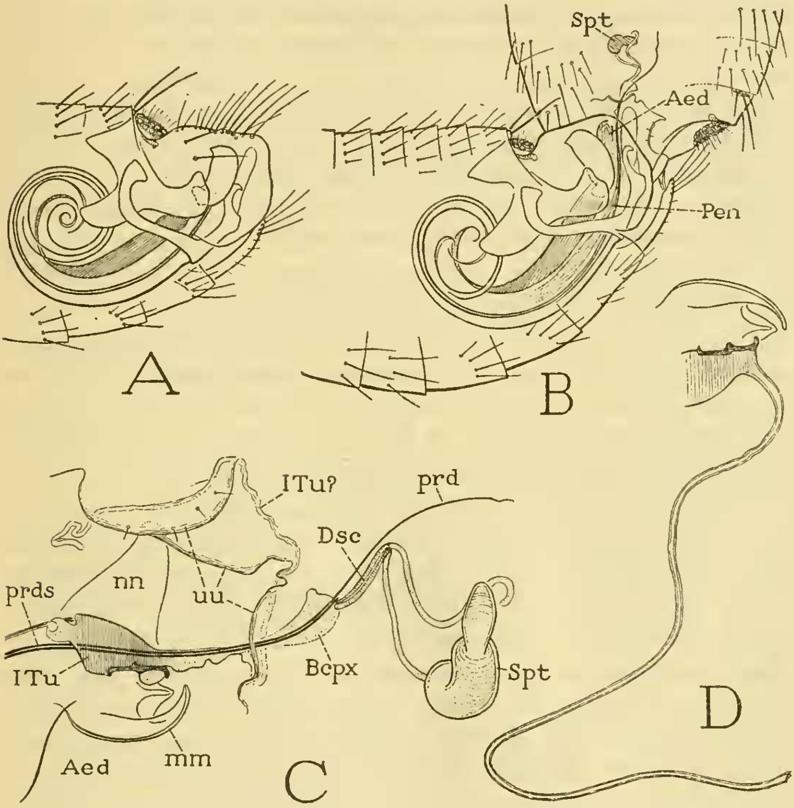

Fig. 8.—Genitalia and copulation of *Ceratophyllus swansoni* Liu.

A, distal part of male abdomen, showing genitalia in position of retraction. B, adjacent parts of abdomens of male and female in copula (from a slide mount lent by Dr. W. L. Jellison). C, details from B, drawn from the opposite side, the female parts (on right) in dorsoventral orientation, the male inverted; showing penetration of penis rods into female. D, inner tube of aedeagus from a mature pupa (same enlargement as C).

Aed, aedeagus; *Bcpx,* bursa copulatrix; *Dsc,* common spermathecal duct; *ITu,* base of inner tube of aedeagus; *ITu?,* apparent external part of aedeagal tube against walls of female genital chamber; *mm,* dorsal apical lobe of aedeagus; *nn,* lateral apical lobe of aedeagus; *Pen,* penis; *prd,* penis rod; *prds,* penis rods; *Spt,* spermatheca; *uu,* wall of female genital chamber.

The internal genitalia of each sex are clearly seen, as are also the claspers and the ninth sternum of the male. For comparison, the organs of the male in the usual retracted position are shown in another specimen of the same species at A. It is to be seen that the aedeagus of the mated male (B, *Aed*) is turned upward, but is protracted only a short distance, and that the coil of the endophallic sack and its rods is only partially unwound. Furthermore, it is plainly demonstrated that the penis rods alone of the male parts have entered the body of the female. The visible details are shown more enlarged at C, drawn from the right side of the specimens, with the female dorsal-side up and the male inverted. The penis rods (*prds*) are projected through the base of the inner tube of the aedeagus (*ITu*) into the bursa copulatrix of the female (*Bcpx*). One rod appears to end at the entrance of the common spermathecal duct (*Dsc*), the other (*prd*) is thrust through the bursal wall and extends far forward in the body cavity of the female. It is not impossible that the penetration of this rod into the haemocoele is a natural procedure, but, on the other hand, it is quite probable that it may be the result of a sudden muscular contraction induced by the killing of the specimens. What is shown conclusively, however, is that the penis rods must be the conveyors of the sperm, since the penis itself is still to be seen entirely within the endophallic sack (B, *Pen*).

A further problem, however, involved particularly in the mating of *C. swansoni,* cannot be so well settled from the mounted specimens. This is the question of what becomes of the long outer part of the aedeagal inner tube (fig. 8 D) of this species, or of others like it. A close examination of the slide shows the tube enveloping the rods where the latter issue from the aedeagus (C). Beyond this point, however, the tube is lost to view except possibly for something that appears to be a strand of delicate tissue (*ITu?*) disposed irregularly in a loop against the wall (*uu*) of the female genital chamber. It would appear, therefore, that the penis rods have been thrust through the wall of the ensheathing tube at the entrance to the bursa, and the tube itself fortuitously cast aside. Truly, the thing does not make sense, but the facts are presented as they have been observed.

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ABBREVIATIONS AND LETTERING ON THE FIGURES

ABBREVIATIONS

Ac, antecosta.
acs, antecostal sulcus.
Aed, aedeagus.
aedAp, aedeagal apodeme.
aedP, aedeagal pouch.
afs, antennal fossa.
An, anus.
Ant, antenna.
Ap, or *ap,* apodeme.
apb, antepygidial bristles.
apl, antepygidial lobes of pupa.
aprd, apodemal rod of endophallus.
astl, anal stylet.
Atr, atrium of spiracle.

Bcpx, bursa copulatrix.

CbP, cibarial pump.
CL, main lobe of genital clasper.
Clp, clypeus.
Clv, clavus.
Cnj, line of conjunctival membrane.
Cor, cornea.
Crc, crochet, aedeagal hook.
ct, clypeal tubercle.
cvpl, cervical plate.
Cvx, cervix, neck.
Cx, coxa.
CxP, pleural coxal process.
CxR, lateral ridge of coxa.

dal, dorsal anal lobe.
Db, ductus bursae.
Dej, ductus ejaculatorius.
Dob, ductus obturatus.
Ds, ductus seminalis (of spermatheca).
Dsc, ductus seminalis communis.
DT, longitudinal tentorial arm (dorsal arm?).

EC, end-chamber of aedeagus.
Enph, endophallus, or endophallic sack.
Ephy, epipharynx.
Epm, epimeron.
Eps, episternum.

F, movable finger of clasper.
F′, accessory finger of clasper.
f, flange.
fc, food canal between stylets.
Fm, femur.
For, neck foramen of head (occipital foramen, or foramen magnum).
Fr, frons.
fs, fossa spiraculi.

GC, genital chamber.
Ge, gena.
GeL, subantennal lobe of gena.
Gpr, gonopore.
Gtr, gonotreme (vaginal orifice of female).

H, head.
hf, head flange.
Hphy, hypopharynx.
hphy, suboral lobe of hypopharynx.

iag, interantennal groove.
iar, interantennal ridge.
isg, intersegmental line.
ITu, inner tube of aedeagus.
IXAc, antecosta of tergum *IX.*
IXSL, sternal lobe of segment *IX.*

L, leg.
Lb, labium.
LbPlp, labial palpus.
Lc, lacinia (maxillary stylet).
Lm, labrum.
LP, lateral plate of aedeagal apodeme.
lpl, intersegmental link plate of thorax (*1lpl, 2lpl,* first and second link plates).
lvr, lever arm of lacinia.

mcl, muscle.
Mmr, mesomere (aedeagal branch of primary phallic lobe).
Mnb, manubrium.
MP, middle plate of aedeagal apodeme.
Mth, mouth (opening into pharynx).
MxL, palpus-bearing lobe of maxilla.
MxPlp, maxillary palpus.

N, notum.
nf, notal flange.
NR, transverse ridge of metanotum.
nvp, nerve passage through foramen of metasternal apophysis.

O, ocellus.
Ob, ostium bursae.
Oc, occiput.
ocu, ocular cup.
Odc, oviductus communis.
Oe, oesophagus.
Osp, ostium spiraculi.

Pdc, pedicel of antenna.
Pen, penis.
Perst, peristome.
PgB, postgenal bridge.
Pge, postgena.
Ph, phragma (*1Ph, 2Ph,* mesothoracic and metathoracic phragmata).
PhL, primary phallic lobe.
Phy, pharynx.
Pl, pleuron.
plf, pleural flange.
Plp, palpus.
PlR, pleural ridge.
PlS, pleural sulcus.
Pmr, paramere.
Pmt, postmentum.
Poc, postocciput.
PoR, postoccipital ridge.
ppgAp, postpygidial apodeme.
Prc, precostal area of tergum.
prd, penis rod.
prds, penis rods.
Prmt, prementum.
Prstm, prestomum.
Ptgr, proctiger (anal lobes of segment *X*).
Pyg, pygidium (sensory area of segment *X*).

rd, rod of closing apparatus of spiracle.
Rect, rectum.
Ret, retina.

S, sternum.
sAp, sternal apophysis.
sc, salivary canal.
Scp, scape of antenna.
Seg, segment.
Sit, sitophore (floor of cibarial pump).
SlDct, salivary duct.
SlO, salivary orifice.
SlP, salivary pump.
Sp, spiracle (*1Sp, 2Sp,* first and second thoracic spiracles; *ISp-VIIISp,* abdominal spiracles).
Spt, spermatheca.
Spz, spermatozoa.
Str, anal struts of larva.

T, tergum.
tAp, apodeme of tergum *IX*.
Tar, tarsus.
TB, tentorial bridge.
Tb, tibia.
tc, trabecula centralis.
Tes, testis.
tf, tergal flange.
Tr, trochanter.
Tra, trachea.

Un, unguis (pretarsal claw).
Utr, unguitractor plate.

Vag, vagina.
val, ventral anal lobe.

XAc, antecosta of tergum *X*.

ALPHABETICAL LETTERING

a, tubercle on head of *Opisodasys*.
b, line of neck attachment on head.
c, tubercle of postoccipital ridge.
d, apical flange of maxillary lobe.
e, notch of labial prementum.
f, flange.
g, supporting basal loop of epipharyngeal stylet.
h, dorsal wall of cibarial pump.
i, membranous lateral wall of cibarial pump.
j, membrane from hypopharynx to base of prementum.
k, hypopharyngeal plate.
l, articular knob of fore coxa.
m, anterior marginal infolding of pronotum.
n, lateral metanotal area below accessory ridge (*r*).
o, pleural peg of mesonotum.
p, mesal ridge of coxa.
q, sternal articular sclerite of coxa.
r, horizontal accessory ridge of metanotum.
s, lobe of notal ridge united with pleural ridge.
t, muscle tendon.
u, posterior marginal ridge of metanotum.
v, base of flange (limit of haemocoele).
w, intersegmental lobe between sternum *VIII* and sternum *IX*.
x, proximal ventral sclerite of segment *X*.
y, tube of imaginal aedeagus in aedeagus of pupa.
z, lobe of segment *X*.
aa, cut lateral edge of anterior wall of female genital chamber.
bb, sclerite below bursal aperture of female.
cc, rod in mesal wall of clasper lobe.

dd, median plate between bases of clasper lobes.
ee, base of aedeagal pouch.
ff, immovable process of clasper lobe.
gg, articular process of clasper finger.
hh, strut from middle plate of aedeagal apodeme forming support for inner tube of aedeagus.
ii, dorsal intramural rod of endophallus.
jj, ventral intramural rod of endophallus.
kk, midrib of lateral plate of aedeagal apodeme.
ll, inner wall of aedeagal end-chamber.
mm, dorsal apical lobe of aedeagus.
nn, lateral apical lobe of aedeagus.
oo, median lobe of strut supporting inner tube of aedeagus.
pp, lateral, fulcral arm of strut supporting inner tube of aedeagus.
qq, dorsal arm of inner tube of aedeagus.
rr, lobe on base of inner tube of aedeagus supporting ventral intramural rod of endophallus.
ss, dorsal plate of inner tube of aedeagus.
tt, sheath of inner tube of aedeagus.
uu, wall of female genital chamber.

EXPLANATION OF PLATES

Plate 1

Examples of Fleas

A, *Pulex irritans* L., female.
B, same, male.
C, *Hystrichopsylla gigas dippiei* Roths., female.
D, *Echidnophaga gallinacea* (Westw.), male.
E, *Ctenocephalides felis* (Bouché), male.
F, *Opisodasys pseudarctomys* (Baker), female.
G, *Echidnophaga gallinacea* (Westw.) female.
H, *Hystrichopsylla gigas dippiei* Roths., female, ventral.

Plate 2

The Head

A, *Pulex irritans* L., female.
B, *Ctenocephalides canis* (Curtis), female.
C, *Ctenocephalides felis* (Bouché), female.
D, *Pulex irritans* L., female, dorsal aspect of head.
E, same, interior view of region of antennal fossae and interantennal ridge.
F, *Hystrichopsylla gigas dippiei* Roths., male.
G, same, female.
H, *Leptopsylla segnis* (Schönherr), female.
I, *Anomiopsyllus* sp., female.
J, same, clypeal tubercle (I, *ct*), anterior.
K, *Hystrichopsylla gigas dippiei* Roths., male with antennae elevated.
L, *Opisodasys pseudarctomys* (Baker).
M, *Echidnophaga gallinacea* (Westw.), female, with labial palpi elevated in feeding position.
N, *Trichopsylla eumolpi* (Roths.), male with elevated antennae.

Plate 3

The Head and Mouth Parts

A, *Opisodasys pseudarctomys* (Baker), ventral aspect of head, mouth parts removed.
B, *Hystrichopsylla gigas dippiei* Roths., male, ventral aspect of head and mouth parts.
C, same, female, ventral aspect of head and mouth parts, with attached cervical sclerites.
D, *Pulex irritans* L., ventral aspect of head.
E, *Ctenocephalides felis* (Bouché), horizontal section of head, seen from below.
F, *Hystrichopsylla gigas dippiei* Roths., female, horizontal section of head, seen from below, showing trabecula centralis (*tc*), longitudinal arms of tentorium (*DT*), and posterior pharynx (*pPhy*).

G, *Anomiopsyllus* sp., horizontal section of head, seen from above, showing bridge and longitudinal arms of tentorium.

H, *Hystrichopsylla gigas dippiei* Roths., female, median vertical section of head and pronotum, mesal view of right half.

I, *Dactylopsylla bluei* (C. Fox), longitudinal arms of tentorium (*DT*) arising from margin of neck foramen, dorsal view.

J, same, muscles attached on back of head and on cervical sclerites.

K, *Pulex irritans* L., cross section of head through eyes (from Hanström, 1927).

L, *Ctenocephalides felis* (Bouché), left antenna.

M, *Pulex irritans* L., anterior view of head and mouth parts.

N, *Hystrichopsylla gigas dippiei* Roths., maxillae and labium, anterior.

O, *Ctenocephalides felis* (Bouché), cross section of head with attached mouth parts, anterior.

PLATE 4

THE MAXILLA

A, *Hystrichopsylla gigas dippiei* Roths., outer lobe and palpus of left maxilla, lateral.

B, same, anterior view of A.

C, *Pulex irritans* L., left maxillary lobe and palpus, lateral.

D, *Dactylopsylla bluei* (C. Fox), left maxilla, lateral.

E, *Anomiopsyllus* sp., right maxilla, mesal.

F, same, apex of maxillary lobe.

G, *Echidnophaga gallinacea* (Westw.), maxillary lobes and palpi, anterior.

H, same, left maxillary lobe and palpus, lateral.

I, *Pulex irritans* L., maxillary lacinia.

J, *Hystrichopsylla gigas dippiei* Roths., apical part of right lacinia, mesal.

K, *Ctenocephalides felis* (Bouché), right maxillary lacinia, mesal.

L, *Hystrichopsylla gigas dippiei* Roths., right maxilla, mesal.

M, *Echidnophaga gallinacea* (Westw.), right maxilla, mesal.

N, same, distal part of left lacinia, lateral.

O, *Pulex irritans* L., right maxilla attached on head, with muscles of lacinial lever, mesal.

P, *Opisodasys pseudarctomys* (Baker), right maxilla, mesal.

Q, *Ctenocephalides felis* (Bouché), distal part of left lacinia, lateral.

R, *Pulex irritans* L., distal part of left lacinia, lateral.

S, *Ctenocephalides felis* (Bouché), right maxilla and muscles, mesal.

PLATE 5

THE LABRUM, EPIPHARYNX, HYPOPHARYNX, AND LABIUM

A, *Pulex irritans* L., labium, anterior.

B, *Hystrichopsylla gigas dippiei* Roths., labium, left side.

C, *Echidnophaga gallinacea* (Westw.), labium, anterior.

D, *Ctenocephalides felis* (Bouché), labium, left side.

E, *Opisodasys pseudarctomys* (Baker), labium, left side.

F, *Echidnophaga gallinacea* (Westw.), labium, left side.

G, Same, labium and stylets, anterior.

H, *Ctenocephalides felis* (Bouché), epipharynx and attached part of pharynx, left side.

I, same, distal part of epipharyngeal stylet, left side.

J, *Hystrichopsylla gigas dippiei* Roths., epipharynx, pharynx, and hypopharynx, left side.

K, *Opisodasys pseudarctomys* (Baker), epipharynx with dilator muscles of cibarial pump on its base.

L, *Pulex irritans* L., epipharyngeal stylet.

M, *Echidnophaga gallinacea* (Westw.), distal part of epipharyngeal stylet.

N, *Hystrichopsylla gigas dippiei* Roths., piece of epipharyngeal stylet, showing posterior flanges and food canal.

O, same, distal part of epipharyngeal stylet.

P, diagrammatic, showing epipharyngeal stylet issuing from head between labrum and hypopharynx.

Q, *Odontopsyllus dentatus* (Baker), base of epipharynx, with overlying labrum, dorsal.

R, *Anomiopsyllus* sp., base of epipharynx, and adjoining part of pharynx; dorsal wall of epipharyngeal loop removed, arrow shows course of food into mouth of pharynx.

S, *Echidnophaga gallinacea* (Westw.), labrum, anterior.

T, *Ctenocephalides felis* (Bouché), hypopharynx and its basal plate, ventral view, showing salivary pump in optical section, and its dilator muscles.

U, same, base of epipharynx with overlying labrum and adjoining part of pharynx, showing thin dorsal wall (*h*) covering basal loop (*g*) of epipharynx.

V, *Pulex irritans* L., hypopharynx and its basal plate, ventral view, showing salivary pump in optical section, and its dilator muscles.

W, *Ctenocephalides felis* (Bouché), hypopharynx and its basal plate, dorsosinistral view, showing sitophore area of plate that forms the floor of the cibarial pump.

PLATE 6

THE EPIPHARYNX AND THE SUCKING APPARATUS

A, *Pulex irritans* L., interior structure of head as seen in a cleared and mounted specimen.

B, same, median vertical section of head, with labium and epipharyngeal stylet, showing cephalic part of food tract and its dilator muscles.

C, *Ctenocephalides felis* (Bouché), the cibarial pump and associated structures, left side; epipharyngeal and hypopharyngeal parts of pump connected by a delicate membrane (*i*).

D, diagrammatic median vertical section of anterior part of head, showing cibarial pump and associated structures; arrows indicate course of food to pharynx.

E, *Pulex irritans* L., cibarial pump, hypopharynx, and salivary pump, left side; lumen of cibarial pump exposed to show its floor (*Sit*) formed by basal plate of hypopharynx.

F, same, section of dorsal wall of head, with cibarial pump, pharyngeal pump, and salivary pump, left side.

G, *Philanthus gibbosus* (F.), example of a well-developed epipharyngeal lobe in the Hymenoptera.

H, *Scolia nobilitata* F., another example of epipharyngeal development in Hymenoptera; the prestomum lies between a long, upper, epipharyngeal lip (*Ephy*), and a similar lobe (*hphy*) on base of hypopharynx.

Plate 7

The Prothorax and the Mesothorax

A, *Hystrichopsylla gigas dippiei* Roths., prothorax and first leg, left side.

B, same, basal part of right fore leg, mesal view, showing trochanteral muscles in coxa.

C, same, base of left fore coxa disarticulated from pleuron.

D, *Ctenocephalides felis* (Bouché), prothorax and fore coxa, left side.

E, *Hystrichopsylla gigas dippiei* Roths., sternopleural plate of prothorax, ventral.

F, same, dorsal view of E.

G, same, left half of pronotum seen from below.

H, *Opisodasys pseudarctomys* (Baker), prothorax and first leg, left side.

I, *Hystrichopsylla gigas dippiei* Roths., spines of prothoracic ctenidium.

J, *Pulex irritans* L., mesothorax, left side.

K, same, mesothorax, anterior.

L, *Ctenocephalides felis* (Bouché), mesothorax and base of middle leg, left side.

M, same, mesothorax and bases of middle legs, anterior.

N, *Opisodasys pseudarctomys* (Baker), mesothorax and middle coxa, left side.

O, *Hystrichopsylla gigas dippiei* Roths., mesothorax and bases of middle legs, anterior.

P, same, mesothorax and base of middle leg, left side.

Plate 8

The Mesothorax and the Metathorax

A, *Ctenocephalides felis* (Bouché) lower part of mesothoracic phragma with first link plates attached, anterior.

B, same, right mesopleuron, mesal surface, showing free pleural ridge, papilla of second spiracle, and pleural articulation of second link plate.

C, *Hystrichopsylla gigas dippiei* Roths., right mesopleuron, mesal surface.

D, *Opisodasys pseudarctomys* (Baker), pleural ridge of left mesopleuron, posterior.

E, same, union of mesonotum with mesopleuron, mesal surface.

F, *Ceratophyllus swansoni* Liu, thoracic pupal skin with wing vestige on middle segment.

G, *Hystrichopsylla gigas dippiei* Roths., mesosternum and sternal apophysis, ventral.

H, *Pulex irritans* L., mesosternum and sternal articulation of coxae, ventral.

I, *Hystrichopsylla gigas dippiei* Roths., mesosternum, left side; arrow indicates nerve passage through foramen of sternal apophysis.

J, *Ctenocephalides felis* (Bouché), mesothorax, ventral.

K, *Pulex irritans* L., metathorax and first abdominal tergum, left side.

L, same, metathorax, anterior.

M, *Hystrichopsylla gigas dippiei* Roths., metathorax and base of hind leg, left side.

N, *Ctenocephalides felis* (Bouché), metathorax, base of hind leg, and first abdominal tergum, left side.

O, *Opisodasys pseudarctomys* (Baker), metathorax and hind coxa, left side.

PLATE 9

THE METATHORAX

A, *Ctenocephalides felis* (Bouché), metanotum and adjoining parts of metepimera, inner surface.

B, same, lateral part of metanotum, outer surface, left side.

C, same, lateral part of metanotum with attached episternum, inner surface, right side.

D, *Pulex irritans* L., lateral part of metanotum united with episternum, inner surface, right side.

E, *Ctenocephalides felis* (Bouché), metanotum and phragma, anterior.

F, *Pulex irritans* L., base of left hind leg, lateral.

G, same, base of right hind leg, mesal view, showing sternal articulation.

H, *Dactylopsylla bluei* (C. Fox), right wall of metathorax and hind coxa, inner surface, showing relation of notal, pleural, and coxal ridges, and epimeral muscle of coxa.

I, *Hystrichopsylla gigas dippiei* Roths., adjoining parts of metanotum and metapleuron, inner surface, right side.

J, *Pulex irritans* L., union of notal and pleural ridges, right side, posterior.

K, *Opisodasys pseudarctomys* (Baker), adjoining parts of metanotum and metapleuron, inner surface, right side.

L, *Hystrichopsylla gigas dippiei* Roths., metasternum and metapleura, ventral (epimera partly cut off).

M, *Pulex irritans* L., cross section of metathorax and hind coxae, posterior, showing strengthening ridges of thoracic and coxal walls, and notal branches of depressor muscles of trochanters.

PLATE 10

THE LEGS

A, *Hystrichopsylla gigas dippiei* Roths., base of left hind leg, lateral view, with coxal and trochanteral muscles.

B, same, base of right hind leg, mesal view, showing coxal, trochanteral, and femoral muscles, except body branches of depressor of trochanter (A, *63b, c, d*).

C, same, base of right hind leg, mesal view, with trochanteral muscles only.

D, *Dactylopsylla bluei* (C. Fox), left hind leg, outer surface, showing lateral (anterior) muscles of tibia and tarsus.

E, same, trochanter, femur, and tibia of right hind leg, inner surface, showing reductor muscle of femur, and mesal (posterior) muscles of tibia and tarsus.

F, same, head, mouth parts, and prothoracic legs, anterior.

G, *Echidnophaga gallinacea* (Westw.), last tarsomere of hind leg, and pretarsal claws, lateral.

H, *Pulex irritans* L., last tarsomere of hind leg, and pretarsal claws with unguitractor plate at their bases, ventral.
I, same, lateral view of H.

PLATE 11

THE FIRST SEVEN ABDOMINAL SEGMENTS

A, *Hystrichopsylla gigas dippiei* Roths., male, abdomen.
B, *Ctenocephalides felis* (Bouché), female, abdomen.
C, same, tergum *II*, flattened.
D, same, sternum *II*, flattened.
E, *Hystrichopsylla gigas dippiei* Roths., male, tergum *I*, flattened.
F, same, small ctenidial spines on tergum *III*.
G, same, female, right half of tergum *II*, flattened.
H, same, male, middle and right half of tergum *III*, flattened.
I, same, male, middle and left half of sternum *III*, flattened.
J, same, male, tergum *VII*, left side.
K, *Pulex irritans* L., female, notch in lower posterior margin of sternum *VII*.
L, *Hystrichopsylla gigas dippiei* Roths., male, middle and right half of tergum *VII*, flattened.
M, same, median posterior part of tergum *VII*, inner surface, showing connection of setal bases with haemocoele (shaded).
N, *Ctenocephalides felis* (Bouché), female, tergum *VII*, flattened.

PLATE 12

THE EIGHTH AND NINTH ABDOMINAL SEGMENTS

A, *Hystrichopsylla gigas dippiei* Roths., female, end of abdomen.
B, same, female, plates of segment *VIII*, flattened, ventral.
C, *Ctenocephalides felis* (Bouché), male, segments *VIII* and *X*, left side (segment *IX* concealed).
D, *Dactylopsylla bluei* (C. Fox), male, tergum *VIII* and sternum *VIII*, left side.
E, *Pulex irritans* L., male, tergum *IX*, left side.
F, *Hystrichopsylla gigas dippiei* Roths., male, sternum *VIII*.
G, same, male, tergum *VIII* and sternum *VIII*, dorsal.
H, *Trichopsylla eumolpi* (Roths.), male, sternum *VIII*.
I, *Dactylopsylla bluei* (C. Fox), male, sternum *VIII*, ventral.
J, *Opisodasys pseudarctomys* (Baker), male, sternum *VIII*, and intersegmental lobes, lateral.
K, same, male, sternum *VIII*, *ventral.*
L, *Hystrichopsylla gigas dippiei* Roths., female, segments *IX* and *X*, left side.
M, same, female, segments *IX* and *X*, posterior.
N, same, male sternum *IX*, lateral.
O, same, sternum *IX*, dorsal.
P, *Ctenocephalides felis* (Bouché), male, sternum *IX*, dorsal.
Q, same, sternum *IX*, lateral.
R, *Opisodasys pseudarctomys* (Baker), male, sternum *IX*, lateral, with attached apodemal rod of endophallus.

Plate 13

The Ninth and Tenth Abdominal Segments

A, *Ceratophyllus swansoni* Liu, male, sterna *VIII* and *IX*, with intersegmental lobe, lateral.
B, *Trichopsylla eumolpi* (Roths.), male, sternum *IX*, lateral.
C, *Dactylopsylla bluei* (C. Fox), male, sternum *IX*, lateral.
D, *Trichopsylla vison* (Baker), male, sterna *VIII* and *IX*, lateral.
E, *Ctenocephalides felis* (Bouché), female, segment *X*, left side.
F, *Hystrichopsylla gigas dippiei* Roths., male, segment *X*, dorsal.
G, same, male, segment *X*, left side.
H, same, female, segment *X*, dorsal.
I, *Echidnophaga gallinacea* (Westw.), male, segment *X* and margin of tergum *IX*, posterior.
J, same, male, dorsal wall of segment *X*, with margin of tergum *IX*, ventral surface.
K, *Opisodasys pseudarctomys* (Baker), female, segment *X*, left side.
L, *Pulex irritans* L., male, segment *X*, posterior.
M, *Ceratophyllus swansoni* Liu, male, segment *X*, ventral.
N, same, female, pupal skin of posterior half of abdomen, with retracted imago within.
O, same, female, pupal skin of segments *VII*, *VIII*, and *X*, posterior.
P, same, adult female, segment *X*, dorsal.

Plate 14

Structure of the Spiracles

A, *Hystrichopsylla gigas dippiei* Roths., first thoracic link plate and spiracle, left side.
B, same, optical section of first thoracic link plate showing trachea and spiracle.
C, *Ctenocephalides felis* (Bouché), first thoracic link plate of right side, mesal view, showing trachea and spiracle.
D, *Hystrichopsylla gigas dippiei* Roths., outer wall of right middle coxa, with associated second link plate and second spiracle, showing coxal muscle of the plate.
E, same, second link plate and second spiracle of left side, lateral.
F, same, second spiracle of left side, ventral.
G, *Ctenocephalides felis* (Bouché), second thoracic link plate and second spiracle, left side, lateral.
H, same, second thoracic spiracle of left side, lateral.
I, same, an abdominal spiracle, left side.
J, *Hystrichopsylla gigas dippiei* Roths., atrium, trachea, and closing apparatus of an abdominal spiracle, right side, mesal.
K, *Xenopsylla cheopis* (Roths.), cross section of closing apparatus of an abdominal spiracle, segment *VI* (from Wigglesworth, 1935).
L, *Ctenocephalides felis* (Bouché), atrium, trachea, and closing apparatus of first abdominal spiracle (in epimeron) of right side, mesal.
M, *Hystrichopsylla gigas dippiei* Roths., first abdominal spiracle of right side, mesal view, opening through flange of metepimeron from haemocoele within the latter.

N, *Ctenocephalides felis* (Bouché), left spiracle of segment *VIII* in lower end of spiracular fossa, with atrium, trachea, and rod of closing apparatus, lateral.

O, *Pulex irritans* L., left spiracle of segment *VIII,* lateral view: optical section of lower end of spiracular fossa, with atrium, trachea, and closing apparatus.

P, same, atrium and trachea of left spiracle reversed, showing rod of closing apparatus on mesal side.

Q, *Opisodasys pseudarctomys* (Baker), female, left spiracle of segment *VIII,* lateral view; spiracular ostium (*Osp*) in deep pit of external fossa (*fs*).

R, same, male, right spiracle of segment *VIII,* mesal view; spiracular ostium (*Osp*) in lower end of long tubular extension (*fs*) of external fossa.

PLATE 15

THE FEMALE GENITALIA

A, *Ctenocephalides felis* (Bouché), female, apical part of abdomen, left side.

B, same, female, end view of abdomen, posterior.

C, same, end of abdomen, left side; genital chamber and vagina exposed by removal of posterior part of tergum *VIII.*

D, *Pulex irritans* L., profile of anterior wall of female genital chamber and sternum *VIII,* exposed by removal of lateral parts of tergum *VIII.*

E, *Ctenocephalides felis* (Bouché), part of genital chamber wall containing bursal aperture, posterior.

F, *Pulex irritans* L., segment *X* and genital chamber wall with bursal aperture, posterior.

G, *Ctenocephalides felis* (Bouché), diagram of receptive parts of female genital apparatus, and mouth of oviduct, left side.

H, same, optical section of bursa copulatrix, anterior view, with spermatheca and ducts shown in same plane, as seen under cover glass.

I, *Hystrichopsylla gigas dippiei* Roths., sperm-receiving system, posterior.

PLATE 16

DISSECTION OF DISTAL SEGMENTS OF MALE ABDOMEN OF *Hystrichopsylla gigas dippiei* Roths.

A, end of abdomen beyond segment *VI,* left side.

B, same, with plates of segment *VII* removed, exposing tergal and sternal plates of segment *VIII.*

C, same, after removal of plates of segment *VIII,* leaving sternum *IX* in place.

D, same, but with segment *X,* sternum *IX,* and aedeagus removed, leaving only tergum *IX* and claspers.

E, segment *X* and mesal surface of right clasper.

F, right clasper more enlarged, mesal surface.

G, claspers and manubria, dorsal.

H, tergum *IX* with claspers and manubria, and segment *X,* dorsal view, flattened.

PLATE 17

THE MALE GENITAL CLASPERS

A, *Ctenocephalides felis* (Bouché), tergum *IX*, left clasper, and segment *X*, left side.
B, same, claspers and manubria, ventral.
C, same, base of right clasper lobe with movable finger, mesal.
D, same, right clasper and manubrium, mesal.
E, *Pulex irritans* L., tergum and sternum of segment IX, with pygidium, left clasper, manubrium, and aedeagal pouch, left side.
F, same, right clasper with base of manubrium, mesal.
G, same, movable finger (*F*) and opposing lobe (*F'*) of right clasper, mesal.
H, *Echidnophaga gallinacea* (Westw.), tergum *IX* with tergal apodeme and genital clasper, and segment *X*, left side.
I, same, right clasper, mesal.
J, *Trichopsylla vison* (Baker), segments *IX* and *X*, with left clasper and manubrium.
K, same, tergum *IX* with claspers and manubria, and segment *X*, dorsal.
L, *Dactylopsylla bluei* (C. Fox), tergum *IX* with apodeme, left clasper and manubrium, and segment *X*, left side.
M, *Trichopsylla eumolpi* (Roths.), tergum *IX* with apodeme, left clasper and manubrium, and segment *X*, left side.

PLATE 18

THE MALE GENITAL CLASPERS AND THE INTROMITTENT ORGAN

A, *Trichopsylla eumolpi* (Roths.), genital claspers and segment *X*, ventral.
B, *Opisodasys pseudarctomys* (Baker), tergum *IX* with apodeme, left clasper and manubrium, and segment *X*, left side.
C, *Thrassis acamantis* (Roths.), right clasper, mesal.
D, *Ctenocephalides felis* (Bouché), intromittent organ, left side; base of aedeagal pouch (*ee*) separates external aedeagus from internal parts.
E, same, aedeagus and its apodeme, with base of endophallus, transparent view showing inner structure, left side.
F, same, penis and penis rods, separated.
G, same, ends of penis rods in natural position.
H, *Echidnophaga gallinacea* (Westw.), intromittent organ, left side.
I, same, end of aedeagus, ventral.
J, same, end of aedeagus, dorsal.
K, same, penis and penis rods, left side.

PLATE 19

THE MALE INTROMITTENT ORGAN

A, *Hystrichopsylla gigas dippiei* Roths., intromittent organ and internal genitalia.
B, same, intromittent organ, left side.
C, same, cross section of aedeagal apodeme.
D, same, cross section of base of aedeagus.

E, same, intromittent organ, showing internal structure of aedeagus.

F, same, dorsal wall of end-chamber of aedeagus with attached endophallic sack, ventral view, showing crochets and inner tube of aedeagus.

G, same, inner tube of aedeagus and its basal support, with attached endophallic sack, left side.

H, same, end of penis, same enlargement as F, I, and J.

I, same, ventral surface of basal support of inner tube of aedeagus, with attached dorsal wall of endophallic sack.

J, same, inner tube of aedeagus with its dorsal plate, and attached ventral wall of endophallic sack containing ventral intramural rod (*jj*).

K, same, penis and penis rods, same enlargement as B and E.

L, same, ends of penis and penis rods, more enlarged.

M, *Pulex irritans* L., outline of male abdomen, showing ordinary retracted position of genitalia.

N, same, intromittent organ, left side, showing gross inner structure of aedeagus.

O, same, aedeagus, showing inner structure as seen in a cleared and mounted specimen.

P, same, cross section of distal part of aedeagal apodeme.

Q, same, the single crochet of aedeagus and its two muscles, dorsal.

PLATE 20

THE MALE INTROMITTENT ORGAN

A, *Pulex irritans* L., coiled inner parts of penis rods and apodemal rod, left side.

B, same, coil of one penis rod isolated.

C, same, penis and penis rods (rods closely attached distally), with enlargement of apical part of penis.

D, same, ends of penis rods more enlarged, left side.

E, same, right side of larger penis rod.

F, *Dactylopsylla bluei* (C. Fox), segments *IX* and *X*, and entire genital apparatus, left side.

G, same, intromittent organ, left side.

H, same, cross section of aedeagal apodeme.

I, same, aedeagus, vertical lengthwise section, showing inner structure and muscles.

J, same, inner tube of aedeagus with its basal support and part of endophallic sack, left side.

K, same, distal parts of penis and penis rods.

L, same, aedeagus, ventral.

M, same, base of inner tube of aedeagus, and its support on median plate of apodeme, dorsal.

N, same, apical armature on sheath of inner tube of aedeagus.

O, same, outline of aedeagus and its apodeme, showing right crochet and its muscle.

P, same, left crochet, lateral.

Q, *Thrassis acamantis* (Roths.), intromittent organ, left side, showing middle plate of apodeme and inner structure of aedeagus.

R, same, left crochet, lateral.

S, *Opisodasys pseudarctomys* (Baker), distal parts of penis rods.

PLATE 21

THE MALE INTROMITTENT ORGAN

A, *Arctopsylla ursi* (Roths.), outline of posterior segments of abdomen, showing genital apparatus with aedeagus projected.

B, *Trichopsylla vison* (Baker), posterior half of abdomen, showing intromittent apparatus as seen in a cleared and mounted specimen.

C, same, intromittent organ, left side.

D, same, aedeagus, showing internal structure.

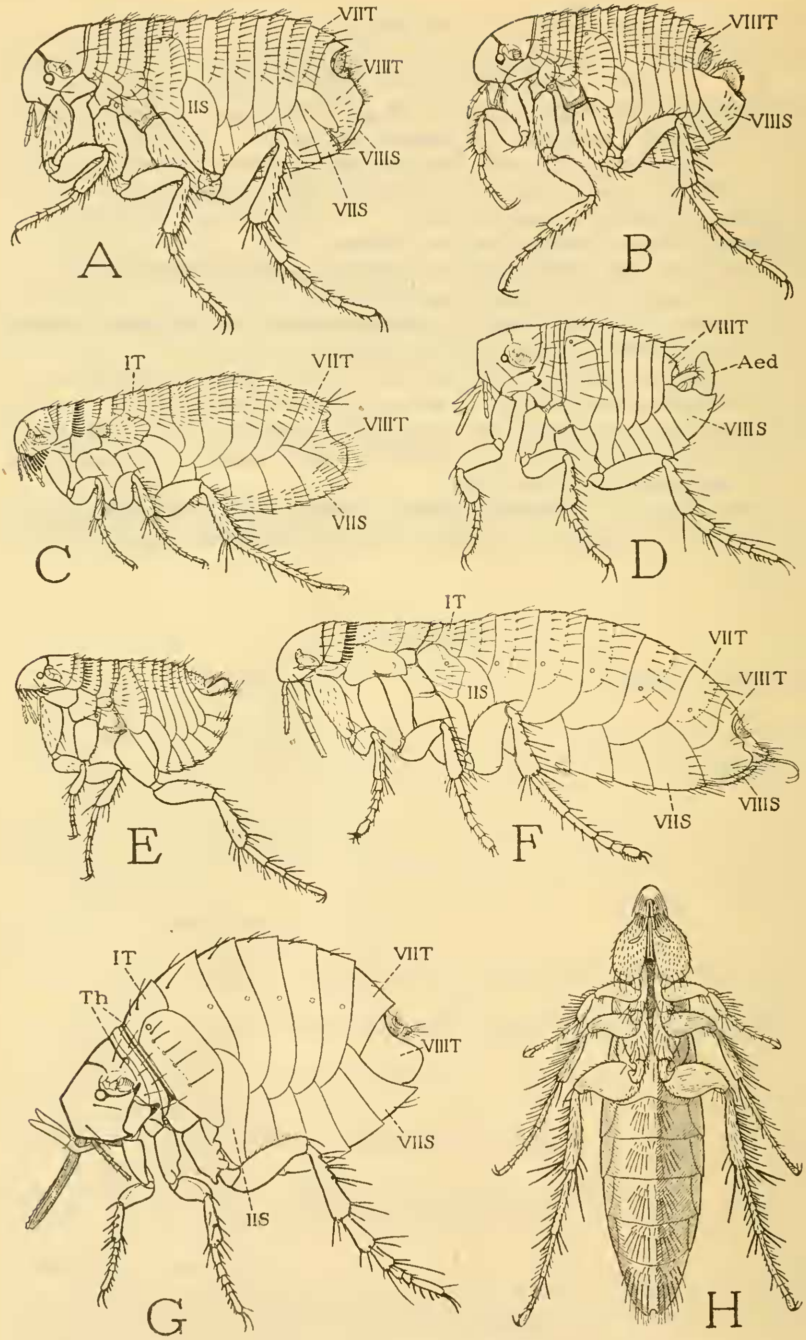
E, same, inner tube of aedeagus, left crochet and its muscle, penis, penis rods, and ventral rod of endophallus, left side.

F, *Trichopsylla eumolpi* (Roths.), intromittent organ, showing inner structure of aedeagus and external part of inner tube.

G, *Ceratophyllus swansoni* Liu, basal part of inner tube of aedeagus and its support on middle plate of aedeagal apodeme, dorsal.

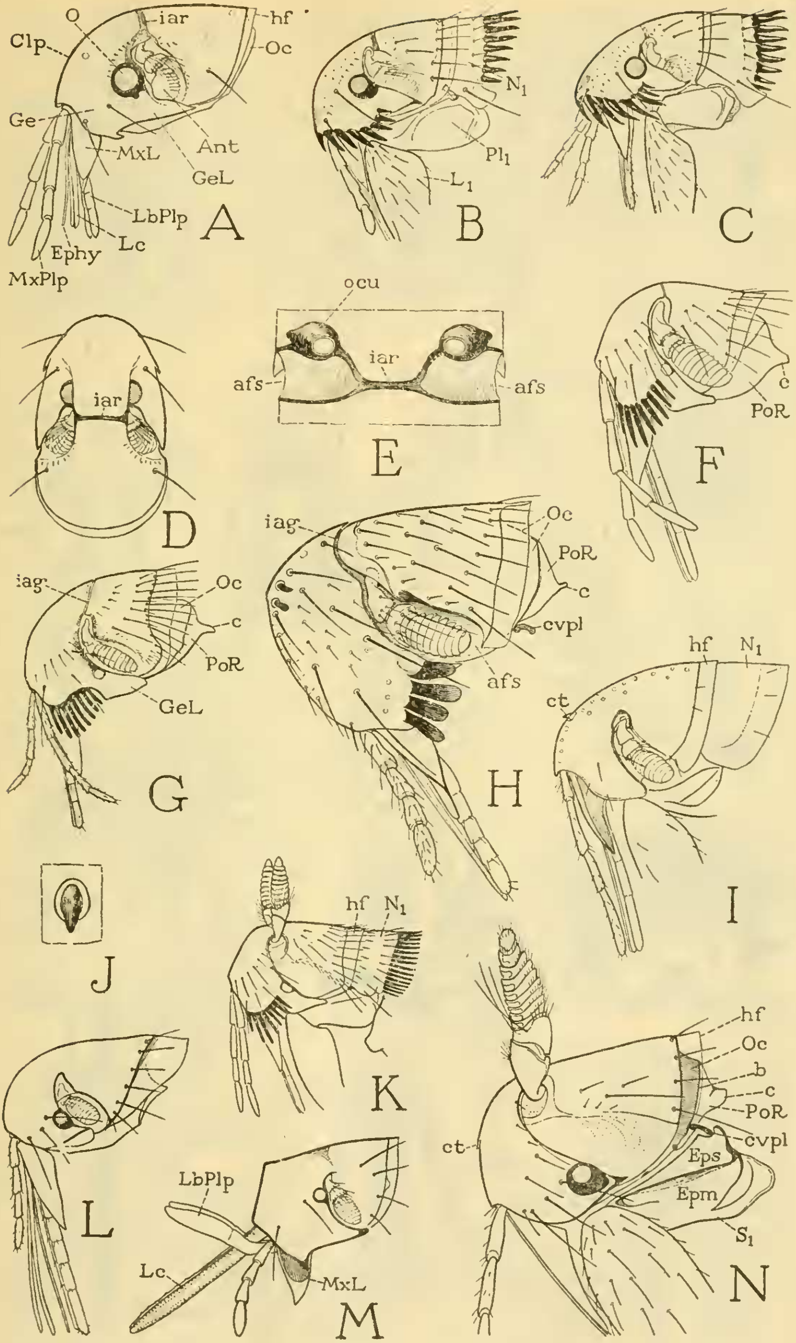
H, same, basal part of inner tube of aedeagus removed from its support, dorsal view, exposing the proximal foramen with attached floor of endophallic sack, and ends of penis rods.

I, same, distal part of intromittent organ, showing inner structure of aedeagus, with long, slender inner tube extending far beyond end of aedeagus.



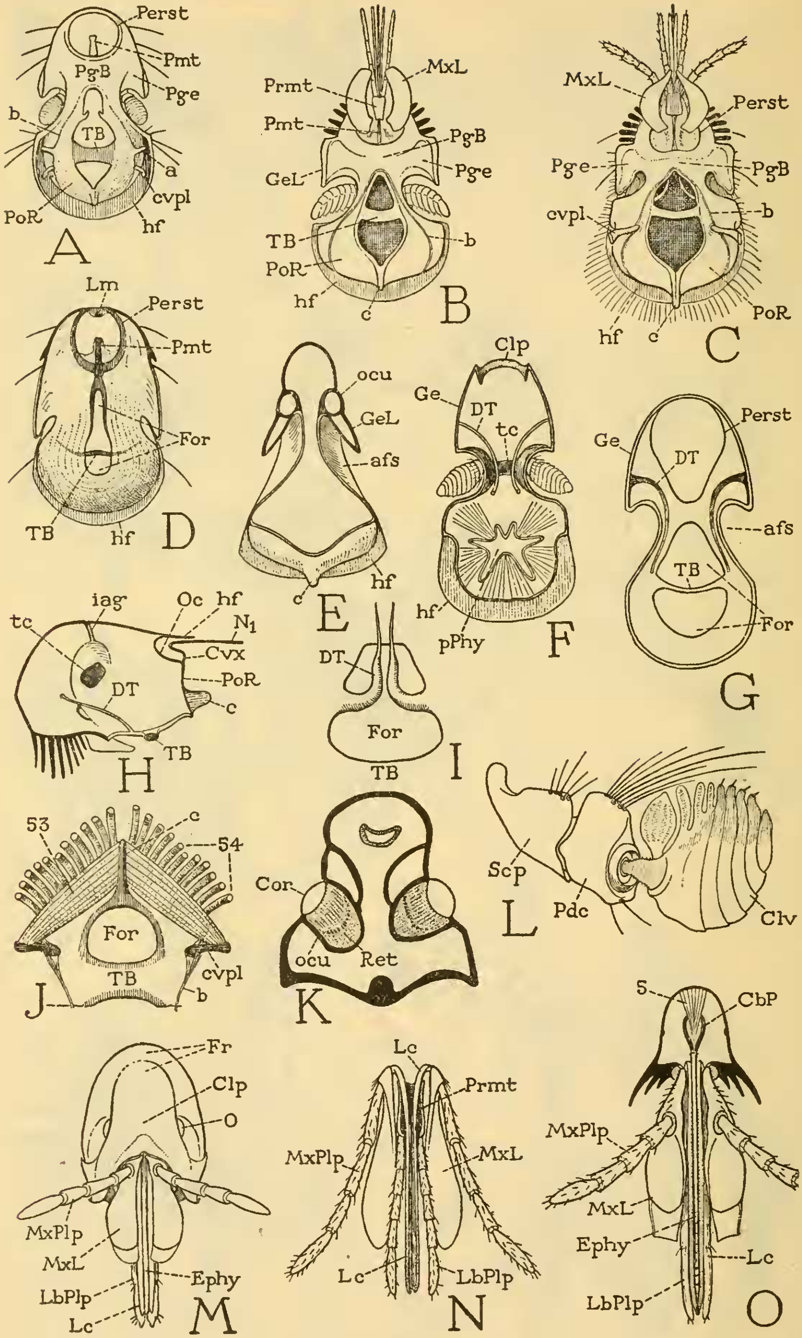
Examples of Fleas

(For explanation, see page 79.)

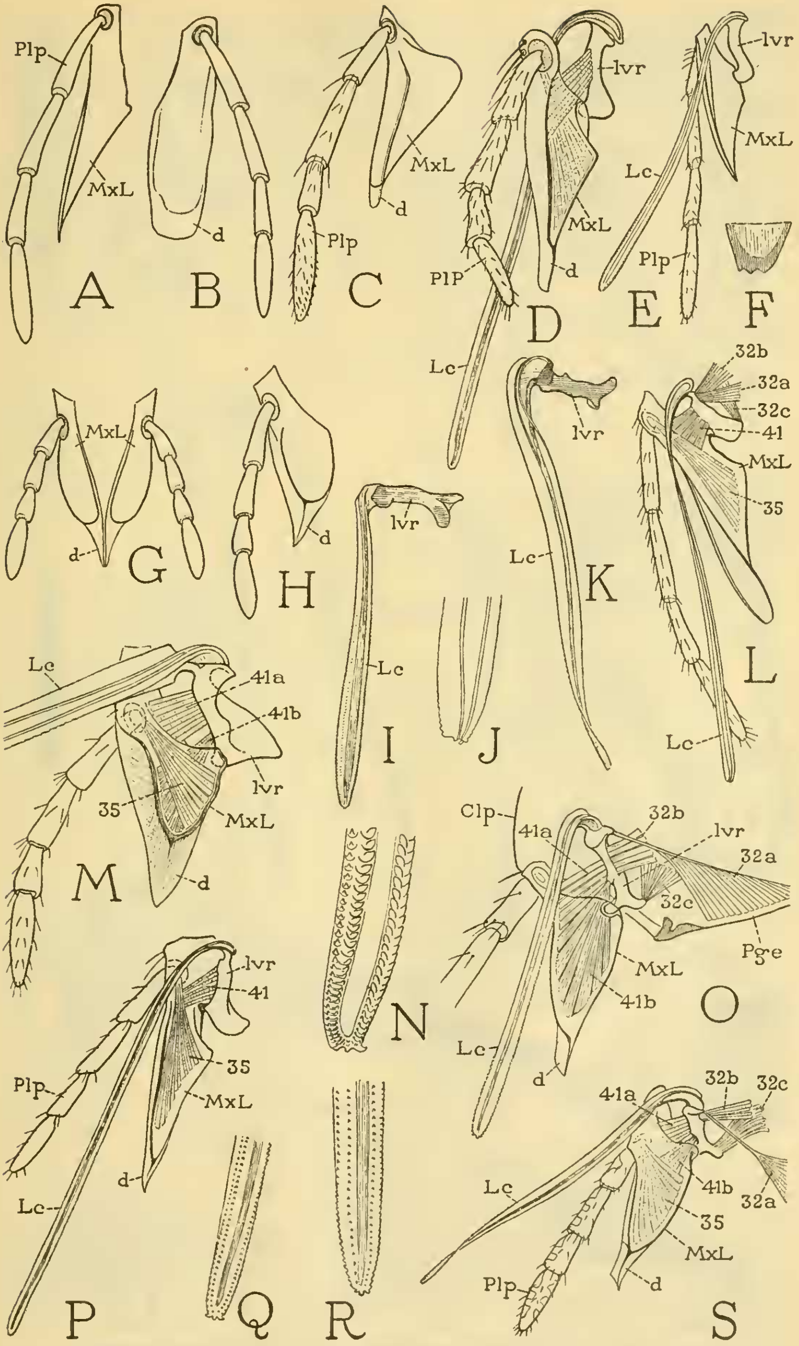


THE HEAD

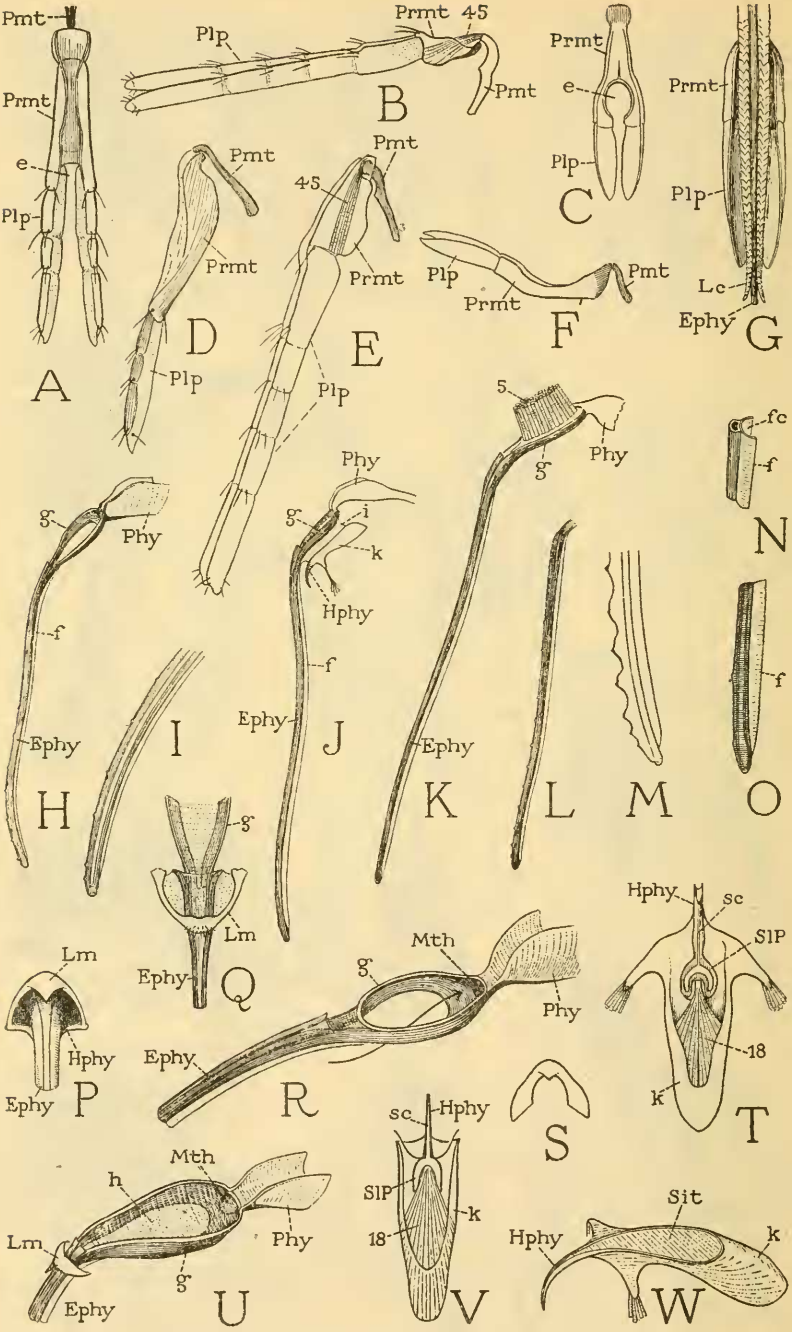
(For explanation, see page 79.)



THE HEAD AND MOUTH PARTS
(For explanation, see pages 79-80.)

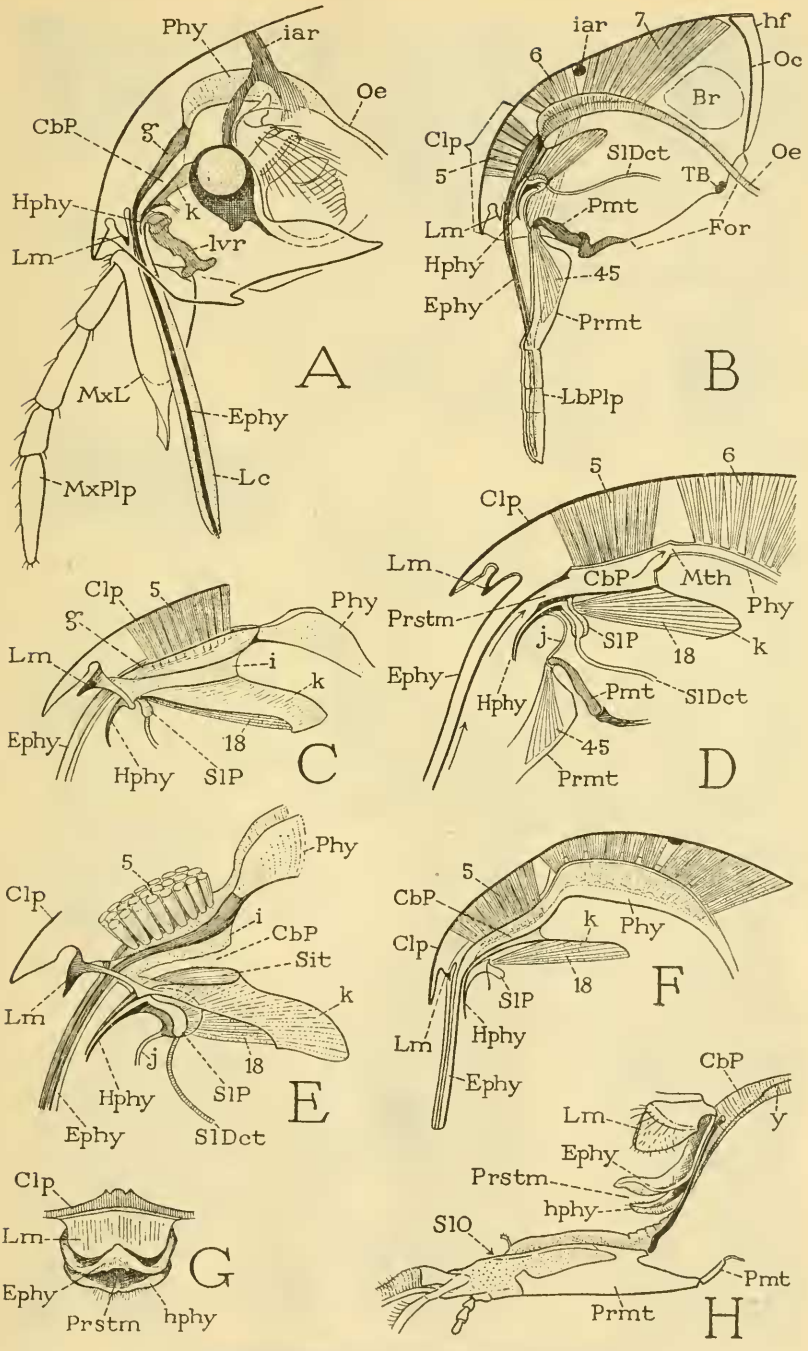


THE MAXILLA
(For explanation, see page 80.)



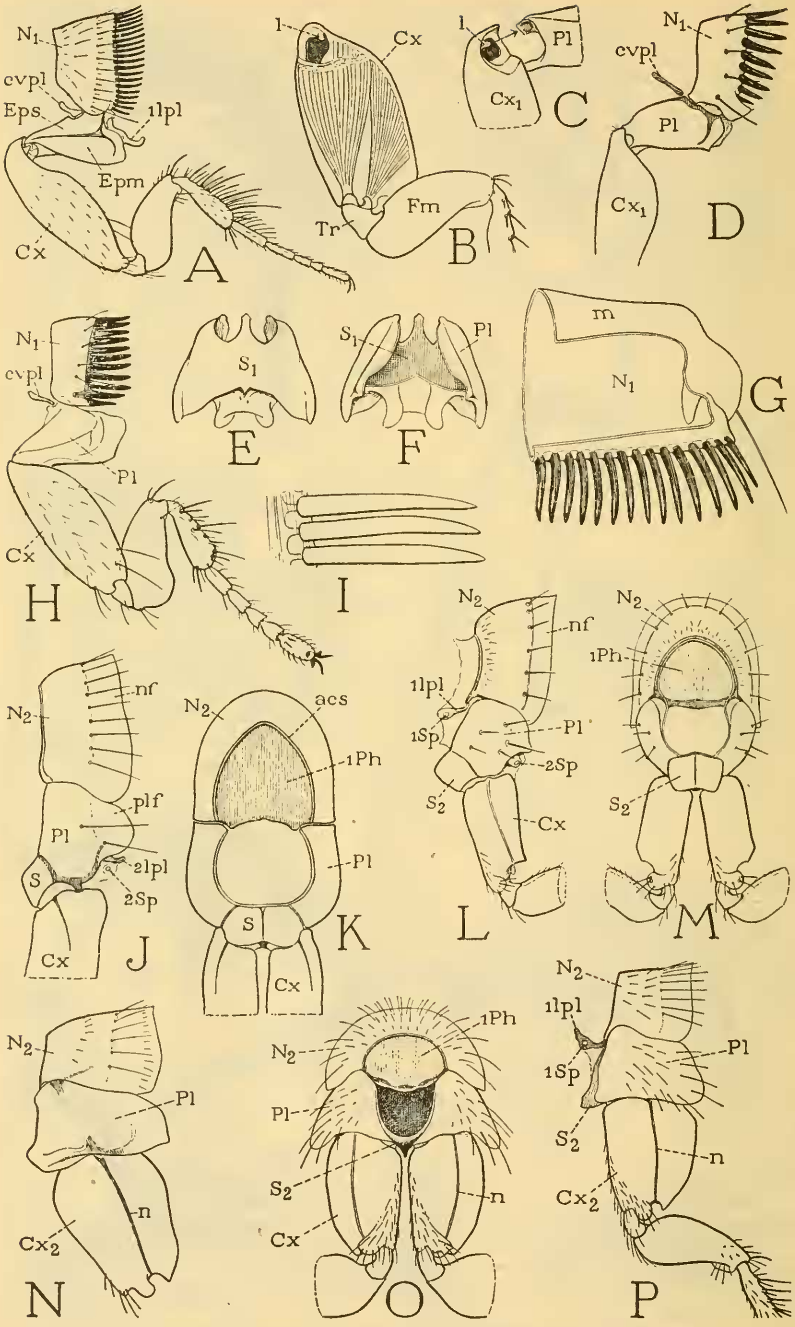
The Labrum, Epipharynx, Hypopharynx, and Labium

(For explanation, see pages 80-81.)



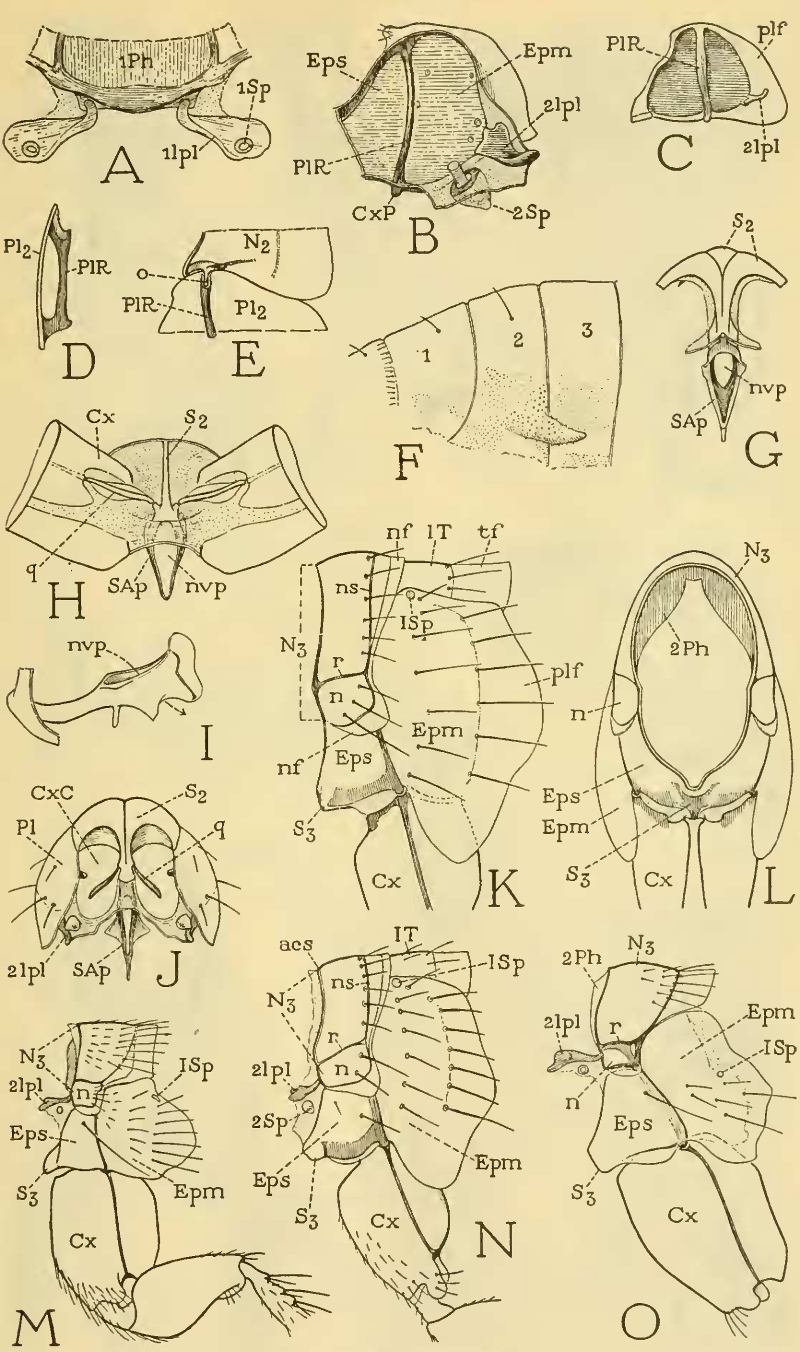
THE EPIPHARYNX AND THE SUCKING APPARATUS

(For explanation, see pages 81-82.)

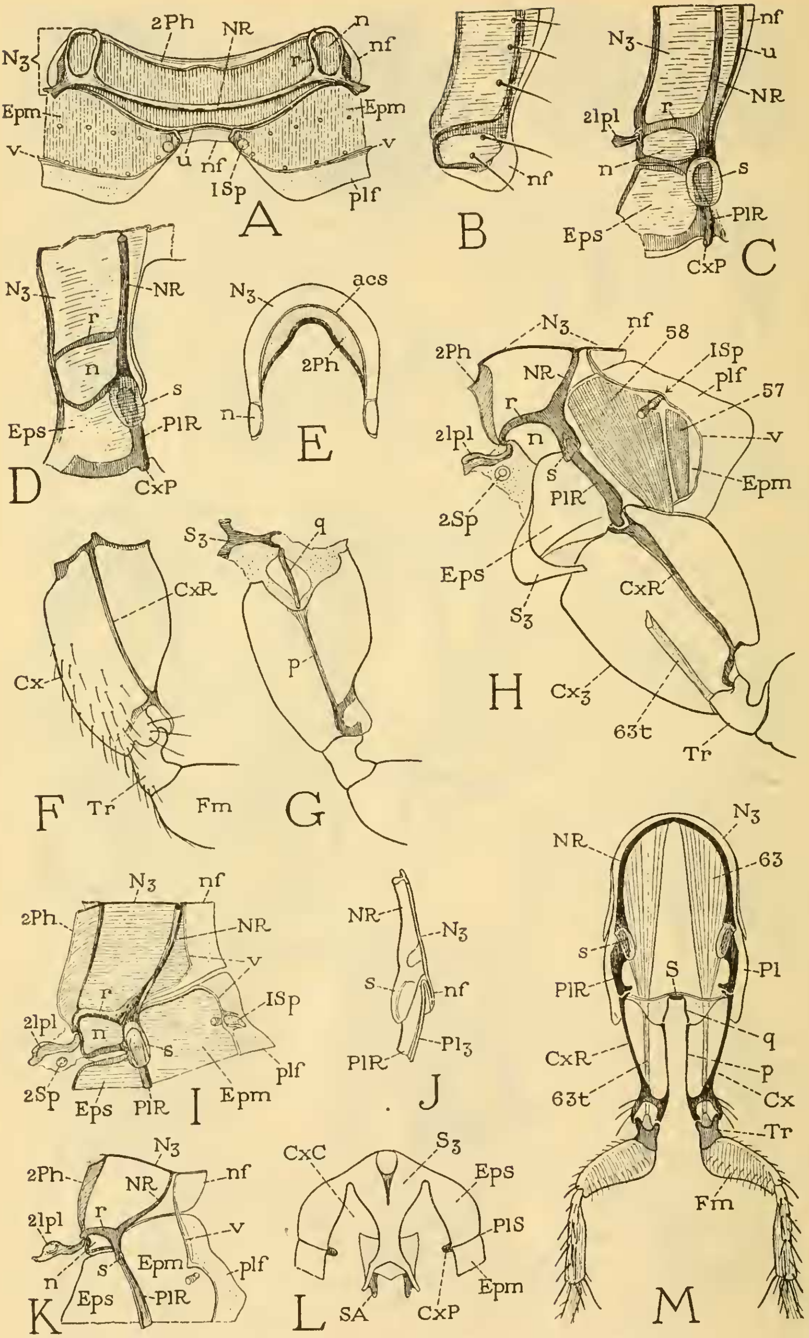


THE PROTHORAX AND THE MESOTHORAX

(For explanation, see page 82.)

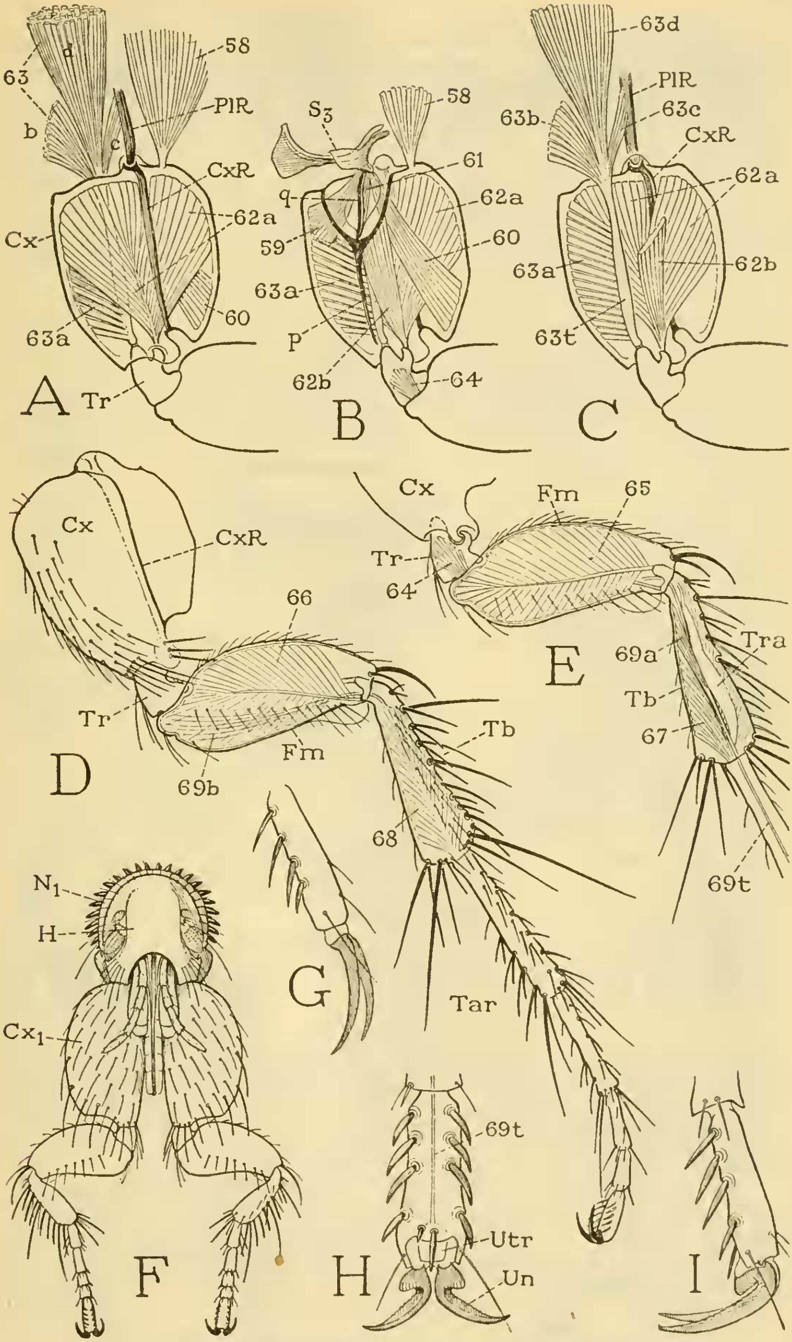


THE MESOTHORAX AND THE METATHORAX
(For explanation, see pages 82-83.)



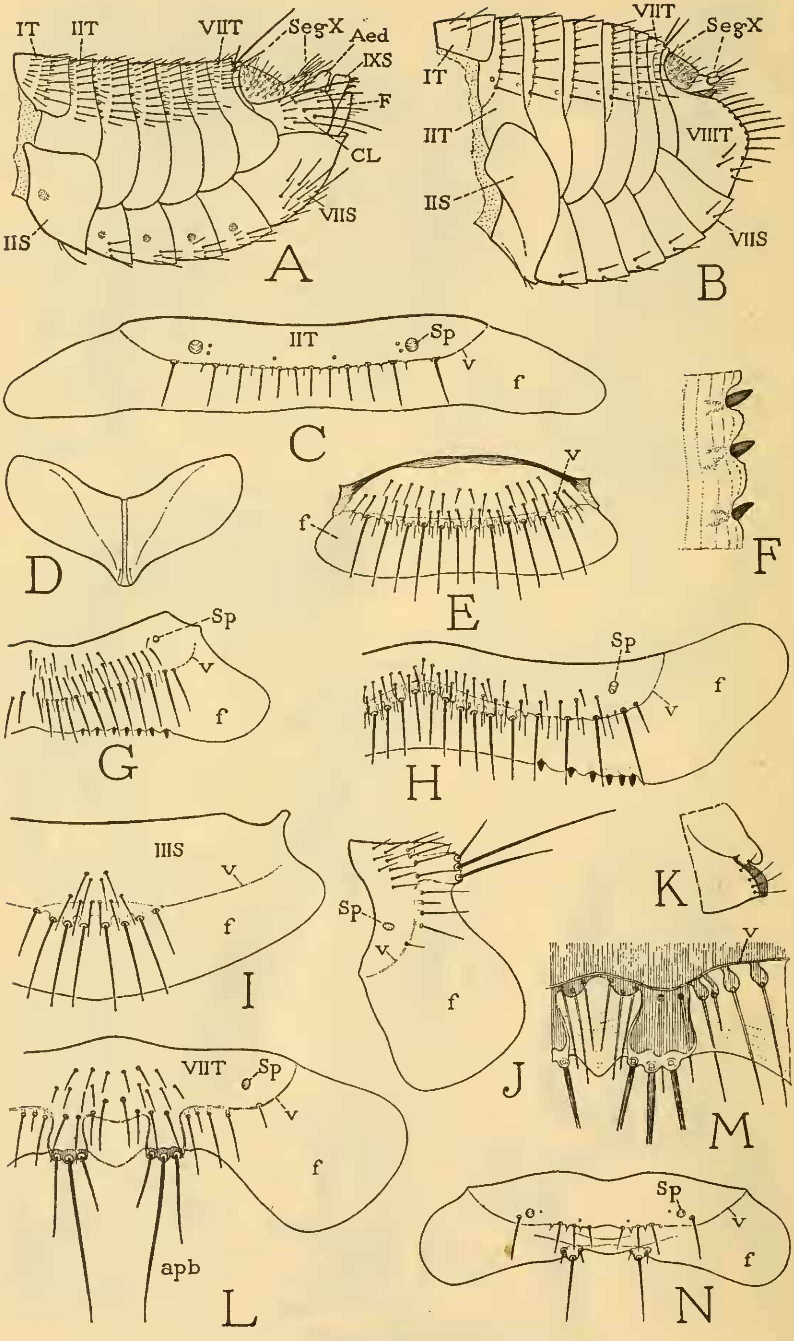
THE METATHORAX

(For explanation, see page 83.)



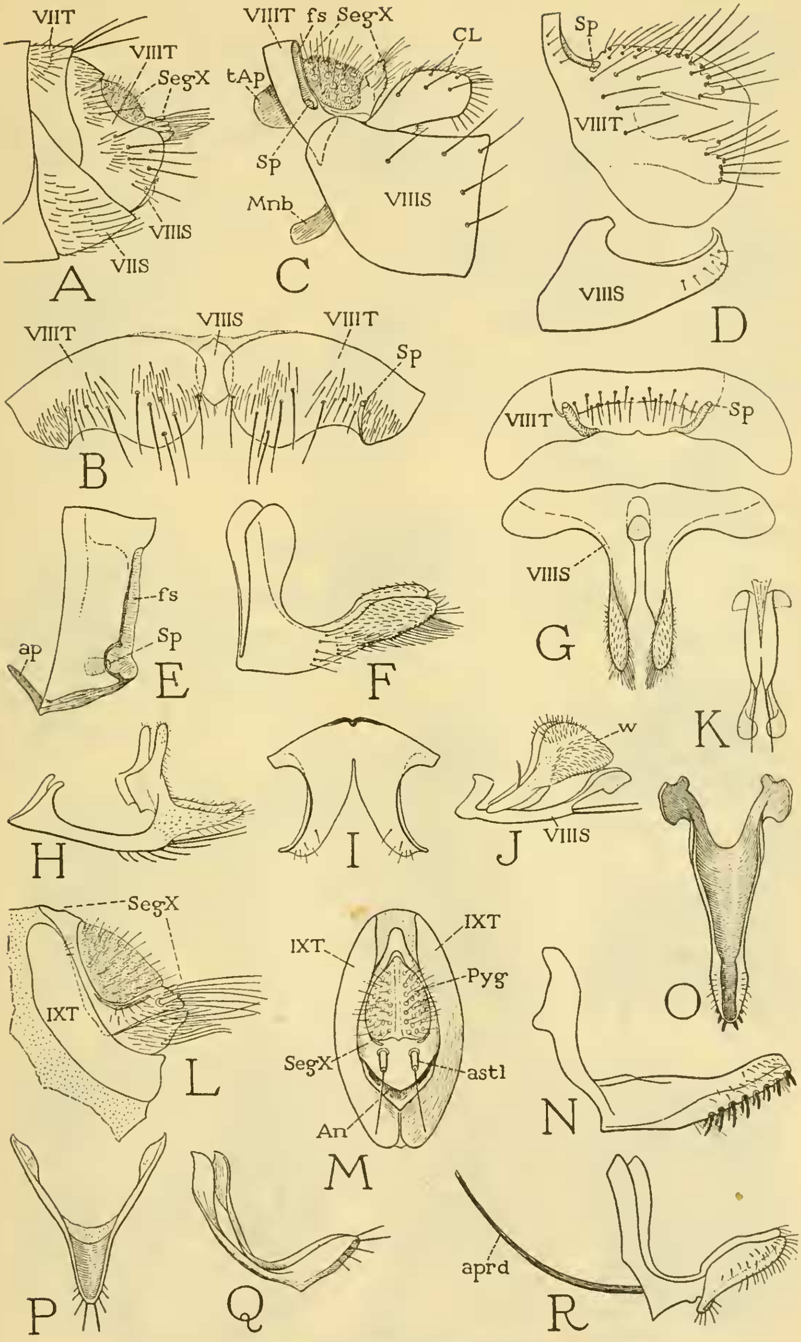
THE LEGS

(For explanation, see pages 83-84.)



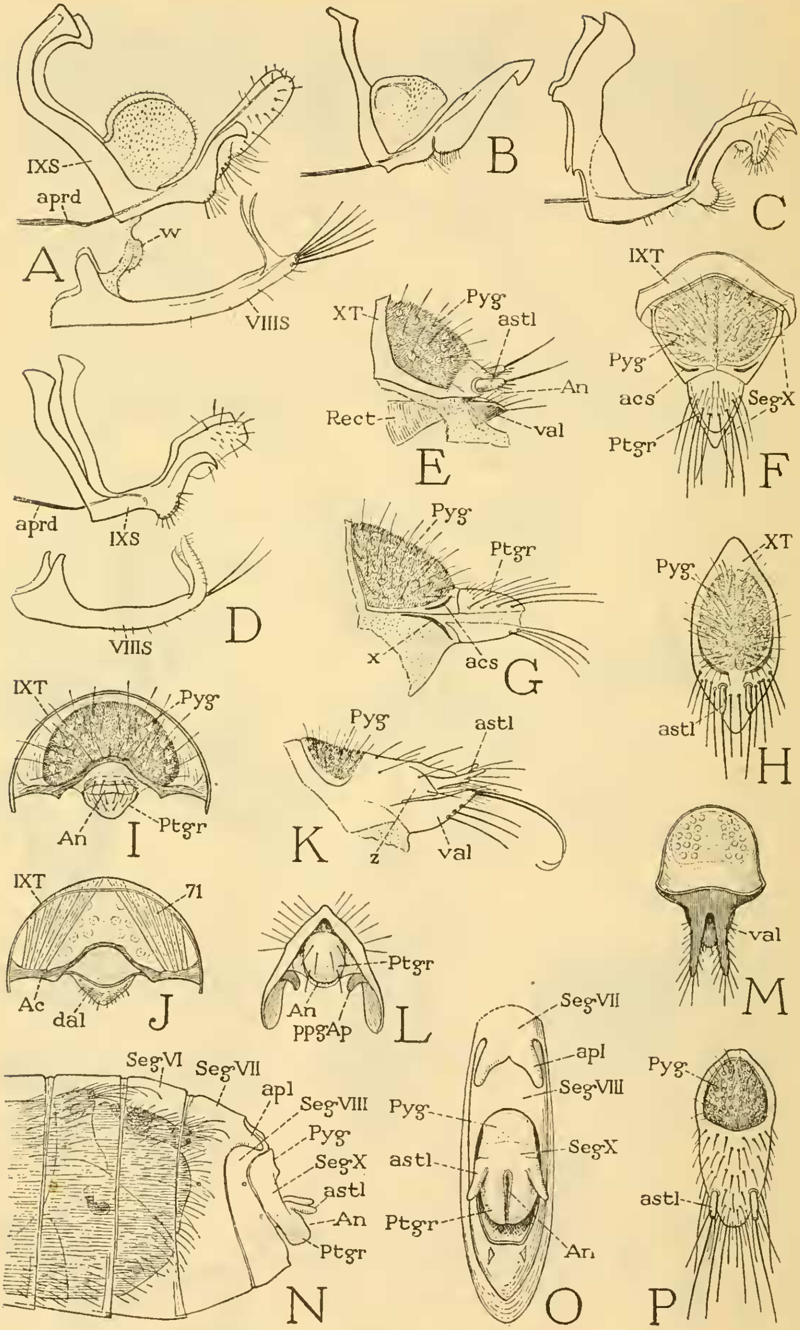
The First Seven Abdominal Segments

(For explanation, see page 84.)



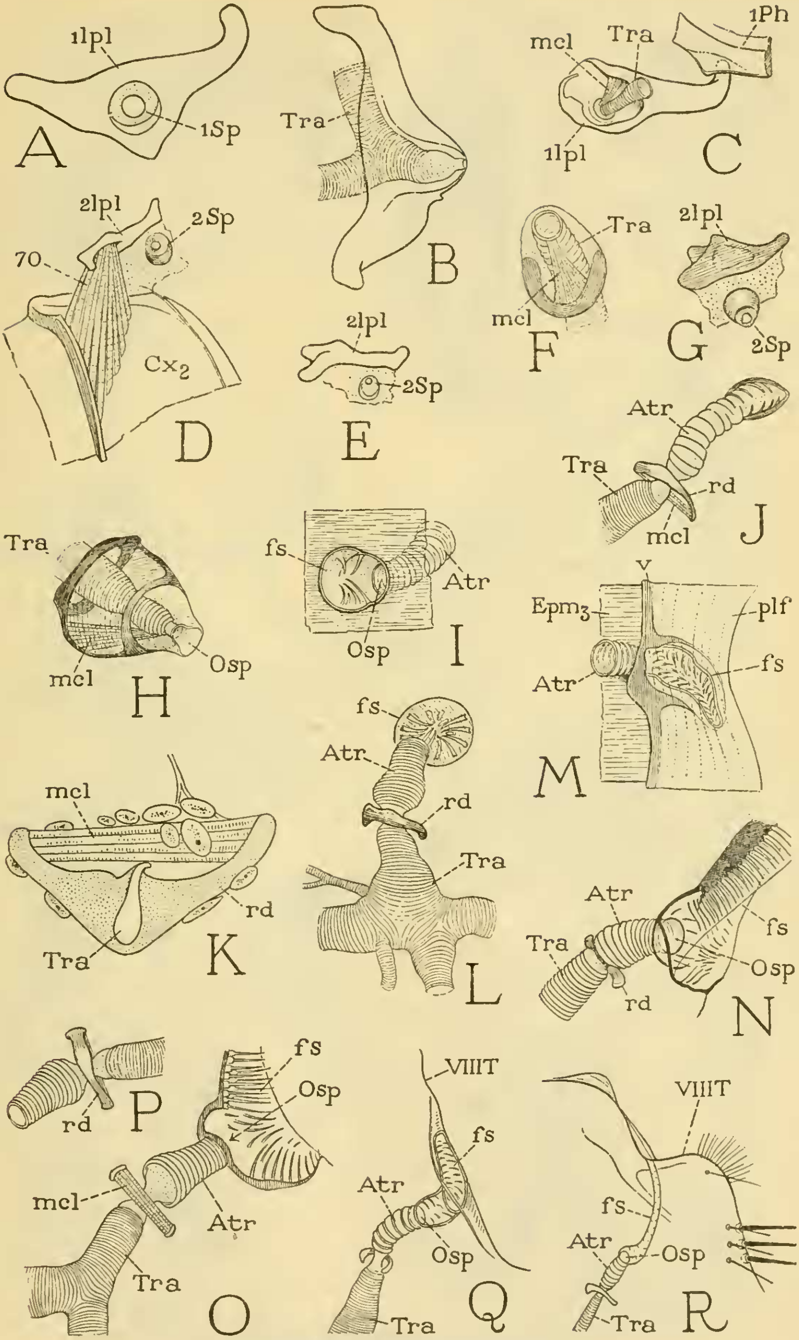
THE EIGHTH AND NINTH ABDOMINAL SEGMENTS

(For explanation, see page 84.)



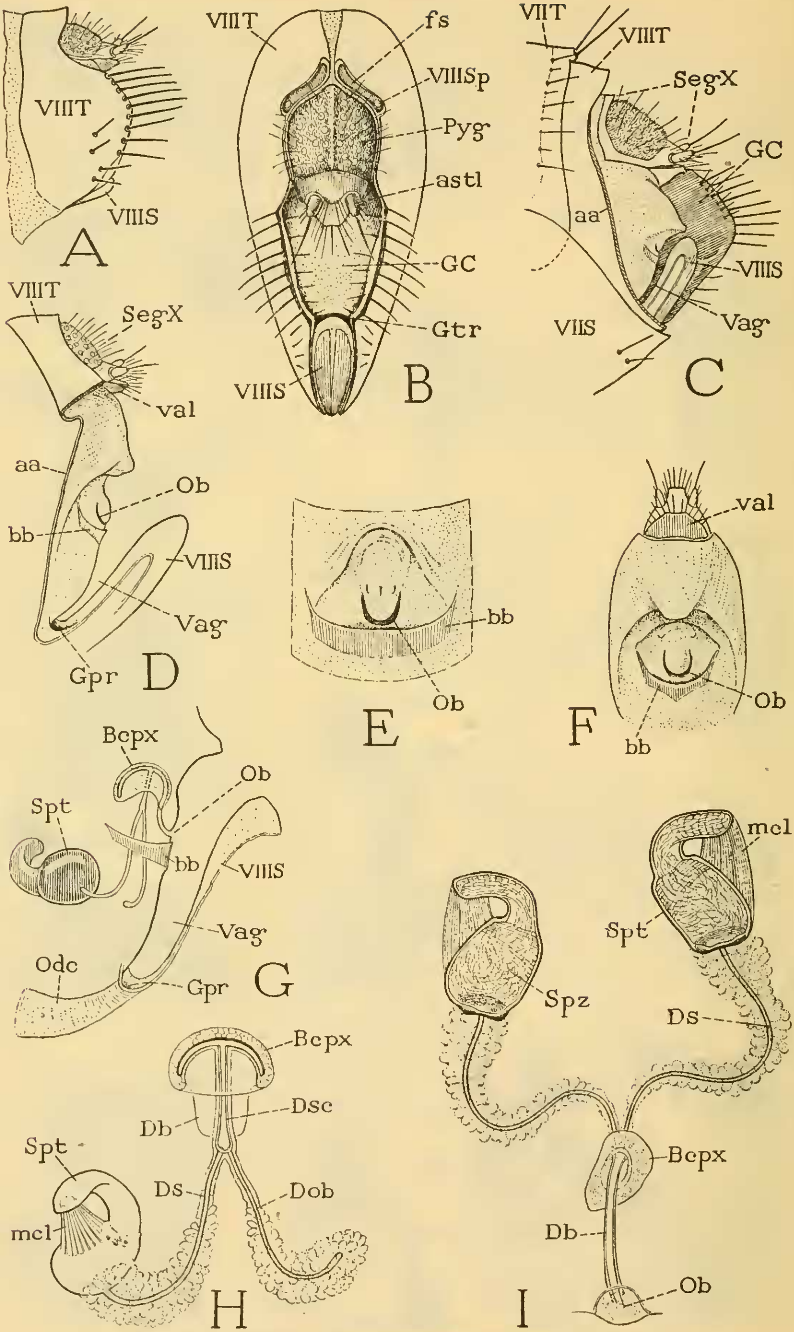
THE NINTH AND TENTH ABDOMINAL SEGMENTS

(For explanation, see page 85.)

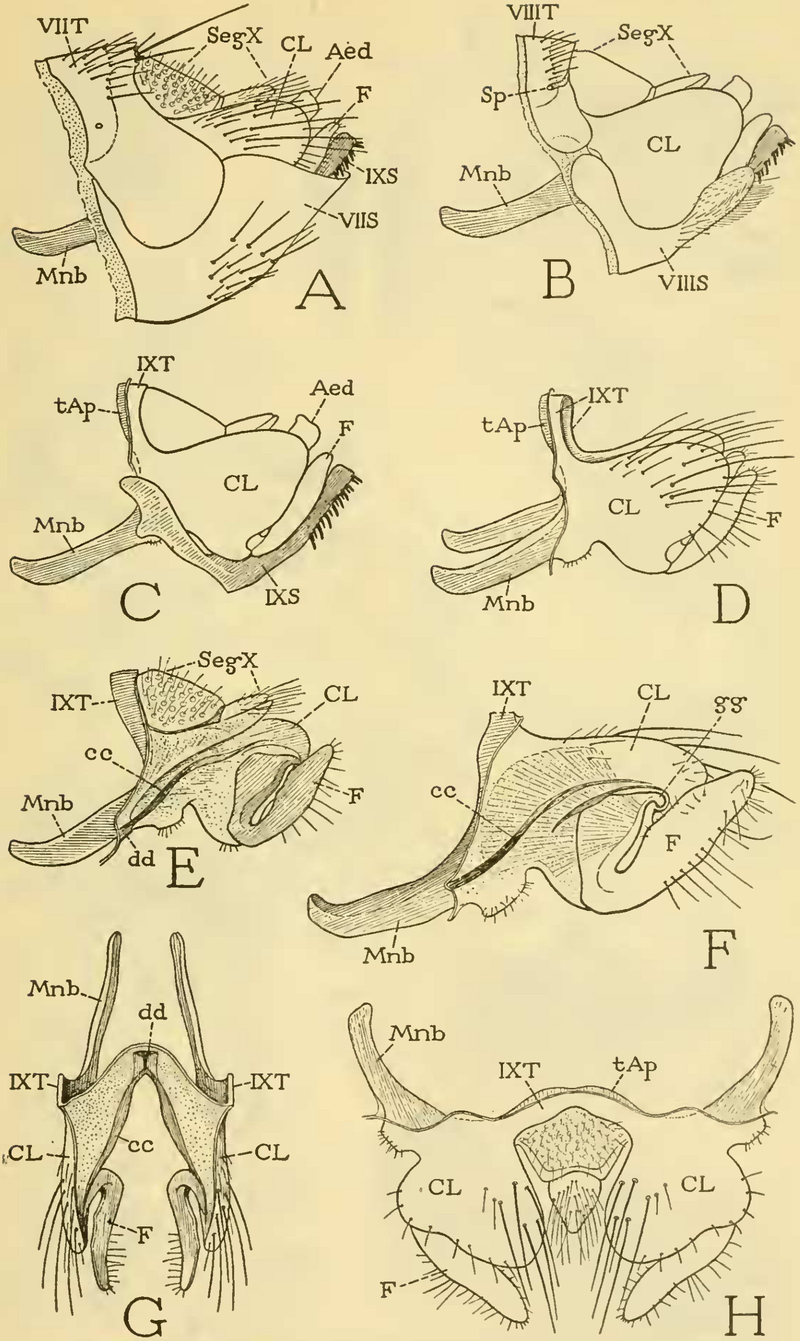


STRUCTURE OF THE SPIRACLES

(For explanation, see pages 85-86.)

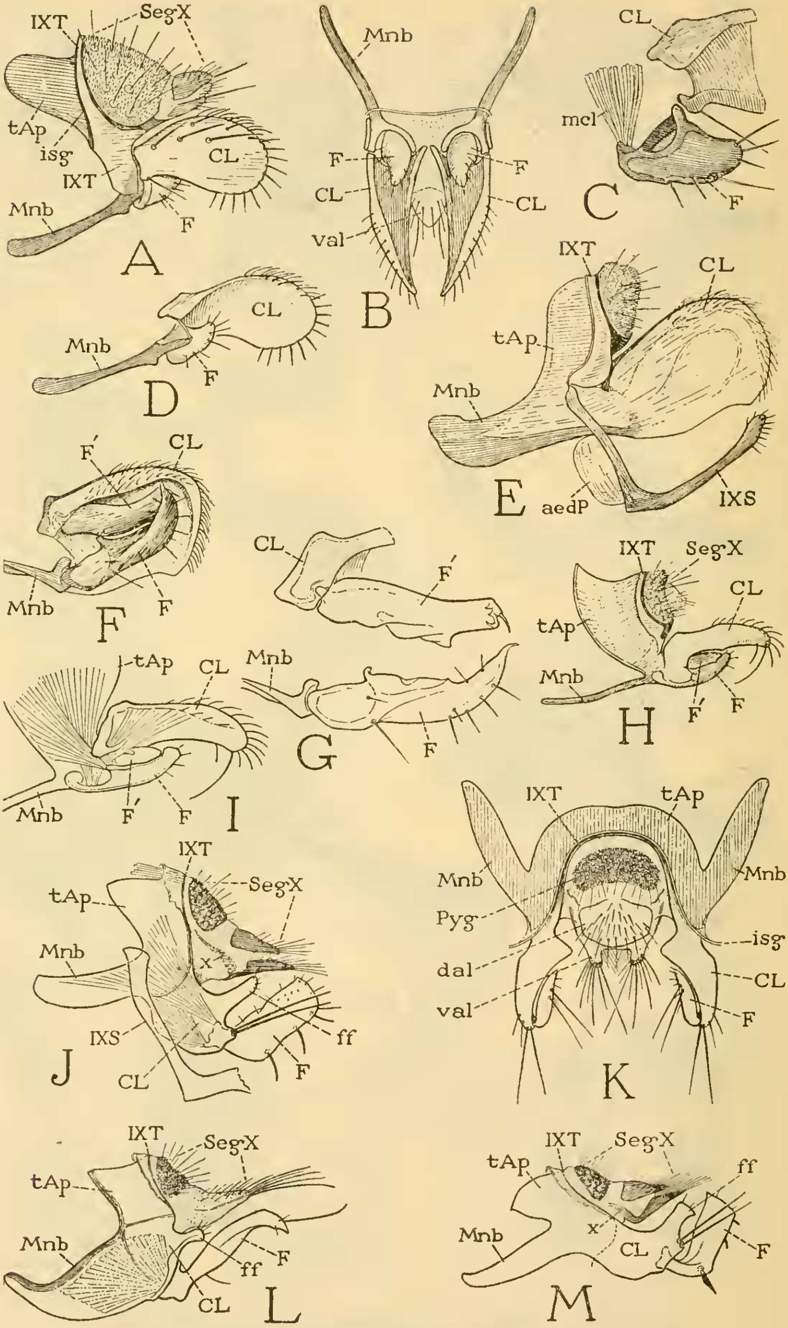


THE FEMALE GENITALIA
(For explanation, see page 86.)



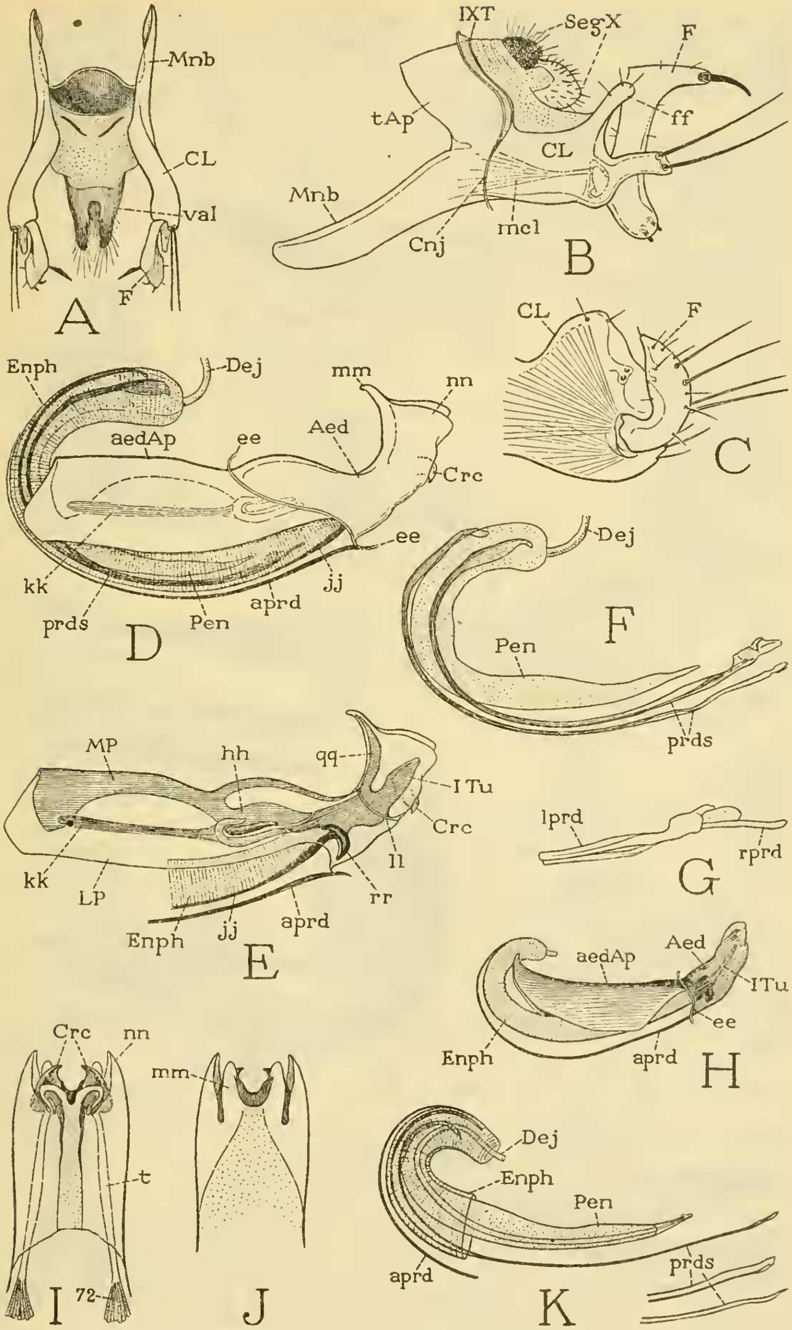
DISSECTION OF DISTAL SEGMENTS OF MALE ABDOMEN OF HYSTRICHOPSYLLA GIGAS DIPPIEI ROTHS.

(For explanation, see page 86.)



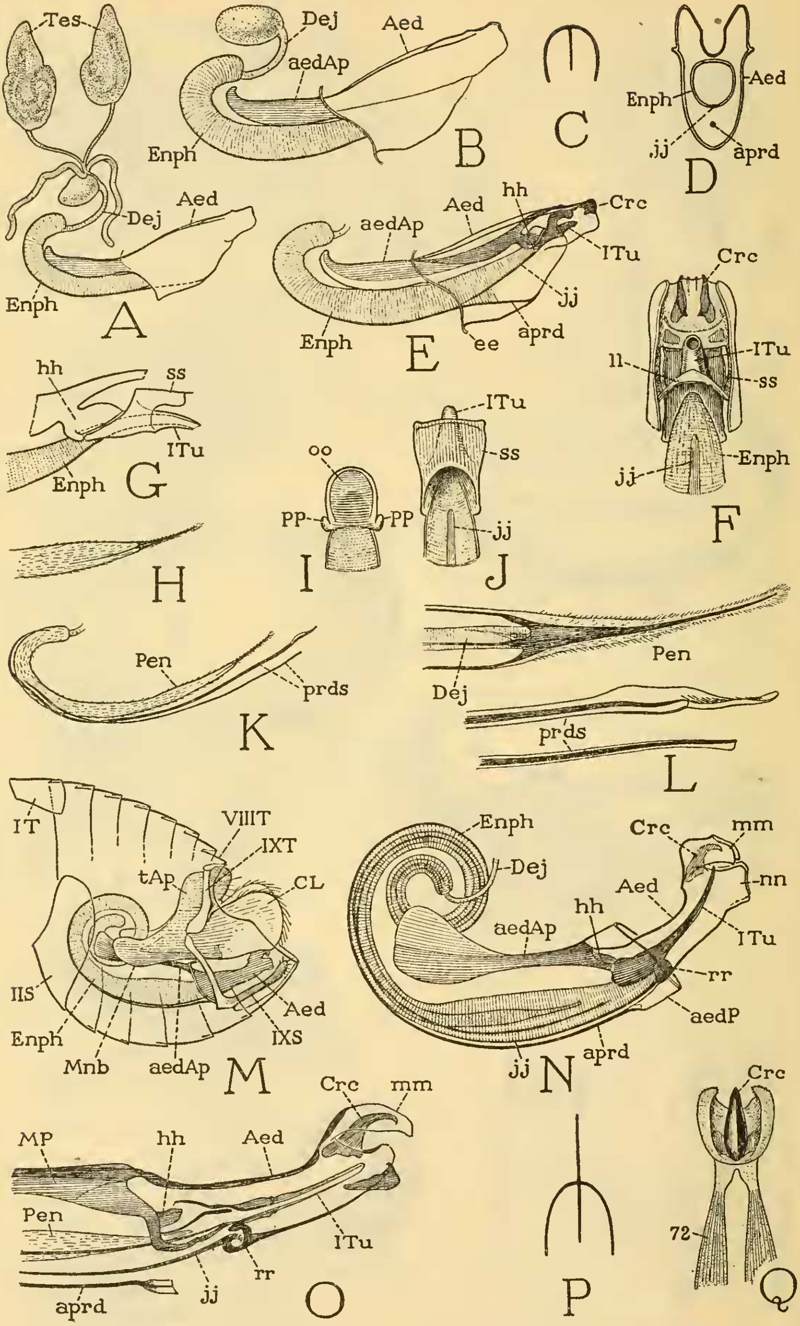
The Male Genital Claspers

(For explanation, see page 87.)

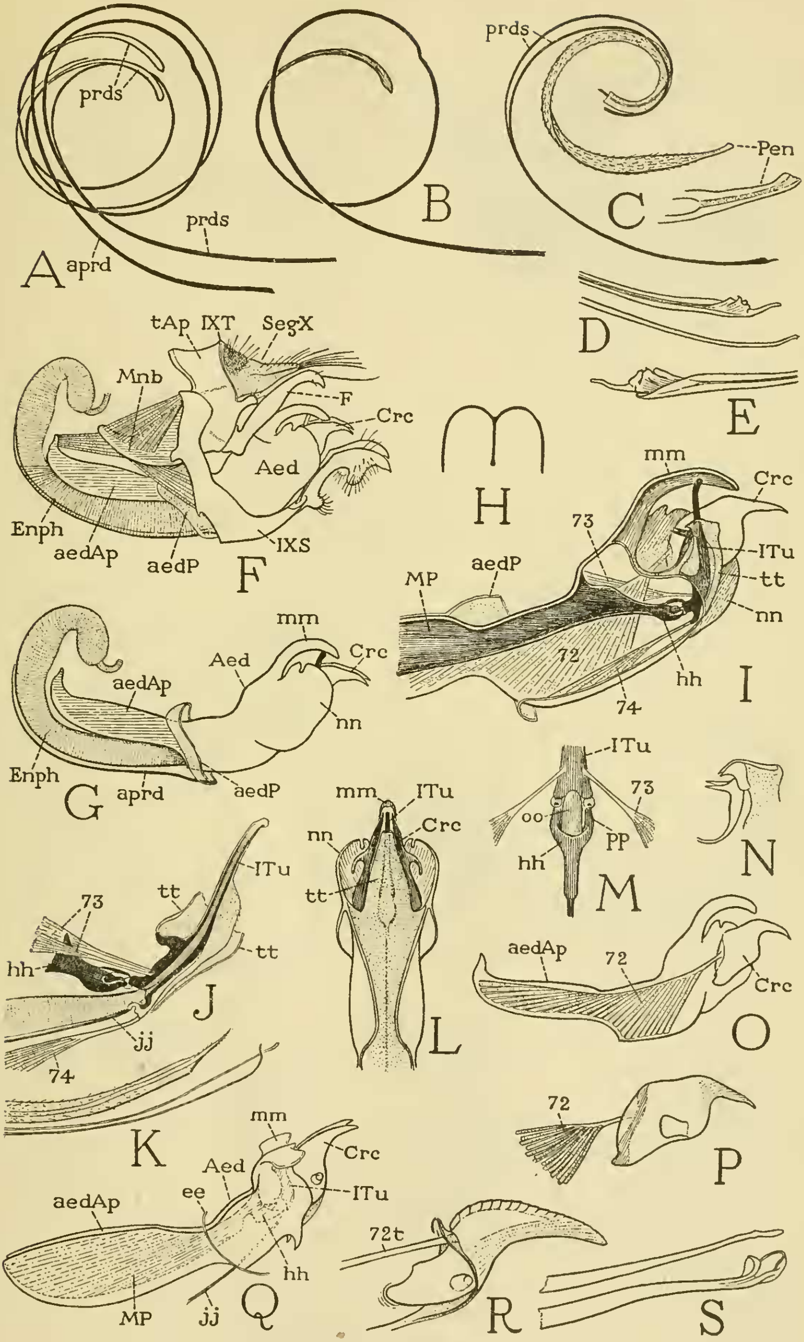


THE MALE GENITAL CLASPERS AND THE INTROMITTENT ORGAN

(For explanation, see page 87.)

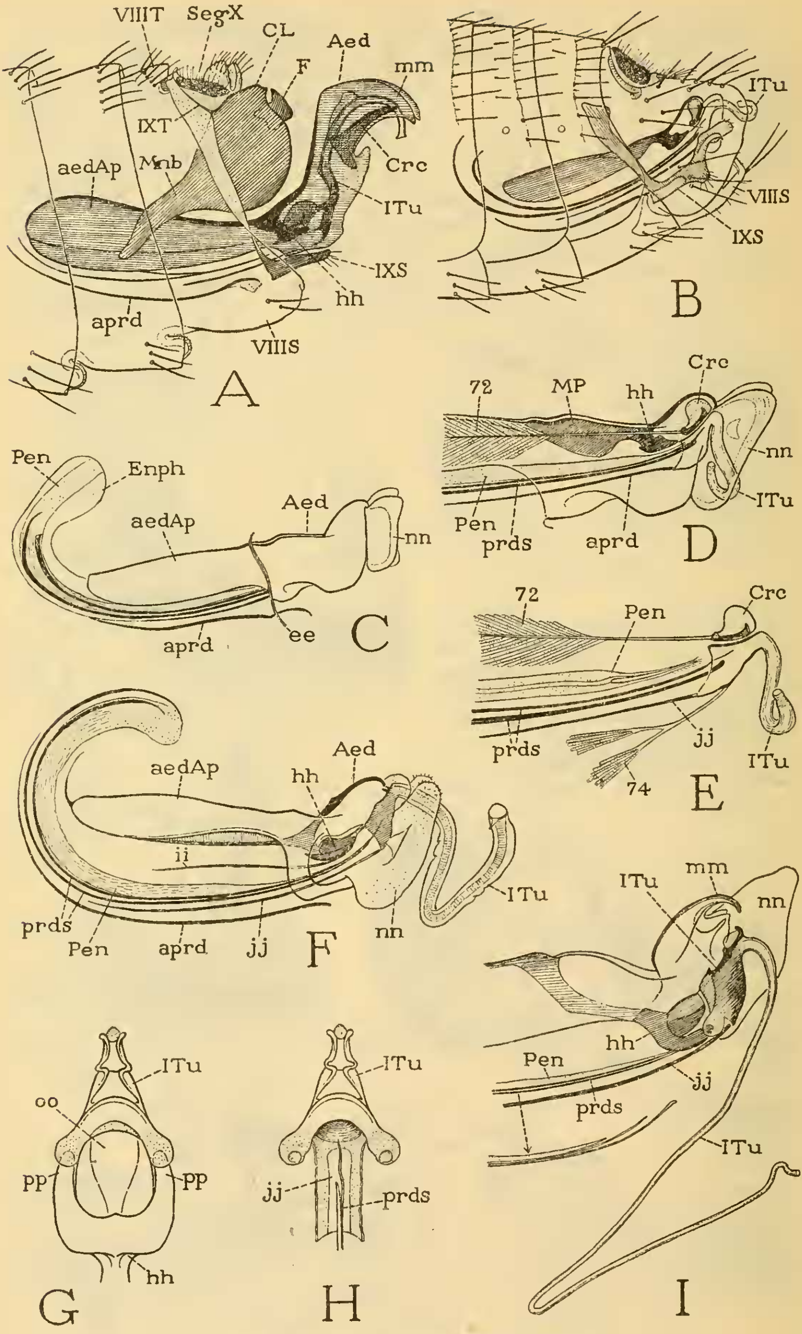


THE MALE INTROMITTENT ORGAN
(For explanation, see pages 87-88.)



THE MALE INTROMITTENT ORGAN

(For explanation, see page 88.)



THE MALE INTROMITTENT ORGAN
(For explanation, see page 89.)